Universidade de Aveiro Departamento de Biologia
2013

Eduardo da Silva Mendes

DIVERSIDADE E ATIVIDADE DE MORCEGOS NO MOSAICO DO BAIXO VOUGA LAGUNAR

BAT DIVERSITY AND ACTIVITY IN THE MOSAIC OF BAIXO VOUGA LAGUNAR

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DIVERSITY AND ACTIVITY OF BATS IN THE MOSAIC OF BAIXO VOUGA LAGUNAR

Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Biologia Aplicada – Ramo de Ecologia, Biodiversidade e Gestão de Ecossistemas, realizada sob a orientação científica do Prof. Doutor Carlos Manuel Martins Santos Fonseca, professor auxiliar com agregação do Departamento de Biologia da Universidade de Aveiro, e coorientação da Doutora Maria João Veloso da Costa Ramos Pereira, investigadora de Pós-Doutoramento do Centro de Estudos do Ambiente e do Mar, da Universidade de Aveiro.

Á Sara…

A toda a minha família…

o júri

presidente

Prof. Doutora Maria Adelaide de Pinho Almeida
professora auxiliar do Departamento de Biologia da Universidade de Aveiro

Doutora Ana Margarida Torres Rainho
chefe de divisão, Instituto de Conservação da Natureza e das Florestas

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agradecimentos

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palavras-chave

Agrícola, *assemblages* de morcegos, Chiroptera, escala, estrutura de paisagem, *guild*, heterogénea, padrões de atividade

resumo

A conversão de ambientes naturais em terrenos agrícolas tem efeitos profundos na composição da paisagem, frequentemente resultando em mosaicos de campos de cultivo, pastagens e restantes fragmentos de vegetação natural. Pensa-se que um aumento na complexidade estrutural de um mosaico de *habitats* pode favorecer a disponibilidade de nichos ecológicos para os animais, potencialmente aumentando a diversidade de espécies. Os morcegos são muito móveis, e muitas espécies requerem o uso de diferentes *habitats* de forma a cumprir as suas necessidades diárias e sazonais. No entanto, a sua distribuição ao longo de uma paisagem pode refletir uma resposta à estrutura da mesma, e às dinâmicas de distribuição espacial e temporal dos recursos, assim como refletir as preferências de alguns *habitats* em detrimento de outros, determinadas pelas características eco-morfológicas da espécie. Desta forma, a seleção de habitat por parte dos morcegos é uma resposta conjunta a características locais e de paisagem. Neste estudo foram investigados os padrões espaciais e sazonais de atividade e diversidade de morcegos numa paisagem heterogénea em Portugal, constituída por um mosaico de *habitats* naturais, semi-naturais e alterados pelo Homem, tanto em ambientes terrestres, como sob a influência de água-doce ou salobra. Além disso, foram investigadas quais as características da paisagem que determinam esses padrões, ao longo de quatro escalas focais distintas. A amostragem de morcegos foi feita acusticamente, enquanto em simultâneo se amostraram insetos usando armadilhas de luz, em 24 pontos representativos dos principais tipos de *habitat* que caracterizam a paisagem. Foi descoberto que as *assemblages* de morcegos dos diferentes *habitats* eram relativamente semelhantes entre si, e que a atividade de morcegos praticamente não diferia entre *habitats*. No entanto, verificou-se a existência de uma forte variação sazonal dos níveis de atividade de morcegos nos vários *habitats*. Além do mais, os resultados obtidos revelaram que a resposta dada pelos morcegos às características locais e de paisagem é dependente da escala e da *guild.* De uma forma geral, os resultados obtidos sugerem que os morcegos exploram todos os *habitats* que constituem esta paisagem heterogénea, e que o mosaico de *habitats* lhes fornece diversas oportunidades, o que resulta em fortes dinâmicas espaciais e sazonais. Por outro lado, foi descoberto que estas dinâmicas são influenciadas por características da paisagem a uma larga escala, assim como por condições meteorológicas, e pela disponibilidade e distribuição locais de recursos. Por último, os resultados indicam que as zonas florestais e o Bocage são potencialmente os *habitats* mais importantes para os morcegos nesta paisagem heterogénea.

keywords Activity patterns, agricultural, bat assemblages, Chiroptera, guild, heterogeneous, landscape structure, scale, Portugal

abstract The conversion of natural environments into agricultural land has profound effects on the composition of the landscape, often resulting in a mosaic of crop fields, pastures and remnant patches of natural vegetation. It is thought that an increase in structural complexity of a habitat mosaic may improve the availability of ecological niches for animals, potentially increasing species diversity. Bats are highly vagile, and many species require the use of distinct habitats to fulfil their daily and seasonal needs. However, their distribution throughout a landscape may reflect a response to landscape structure and spatial and seasonal dynamics of resource distribution, as well as preferences for some habitats relative to others, determined by species eco-morphological traits. Therefore, the way bats select a habitat is an aggregative response to both landscape and local features. We investigated the spatial and seasonal patterns of bat diversity and activity within a heterogeneous landscape in Portugal, constituted by a mosaic of natural, semi-natural and human-altered terrestrial, freshwater and brackish habitats. Furthermore, we investigated which landscape features determine those patterns, across four distinct focal scales. We sampled bats acoustically, while simultaneously sampling insects with light traps, across 24 sampling sites representative of the main habitat types that shape the landscape. We found bat assemblages of the different habitats to be relatively similar, and that bat activity hardly differed among them. However, we found seasonal variation in bat activity within habitats. Additionally, our results revealed both scale- and guild-dependent responses of bats to landscape and local features. Overall, our results suggest that bats exploit all habitats of this heterogeneous area, and that the mosaic landscape provides them several opportunities, which results in strong seasonal and spatial dynamics. On the other hand, we found these dynamics to be influenced by broad-scale landscape features, as well as by weather conditions, and local resource availability and distribution. Lastly, our results indicate that forest and *Bocage* habitats are potential keystone structures for bats within this heterogeneous landscape.

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Chapter 1

General Introduction

1. GENERAL INTRODUCTION

1.1 BAT DIVERSITY

Bats, Chiroptera, are the second mammalian order in terms of number of species (ca. 1300), only surpassed by rodents (ca. 2300, Wilson and Reeder, 2005). The ability to fly actively and to echolocate, the long life-span, the long viability of the sperm cells, and the diversity of ecological niches conquered, are some of the traits that distinguish bats from the other mammalian orders (Dietz et al., 2009). The dietary habits of bats range from animalivory (arthropods, small vertebrates and blood) to herbivory (nectar and pollen, fruits and leaves) (Patterson et al., 2003), and they occur throughout the world with the exception of the Arctic, Antarctica and some oceanic islands (Findley, 1993; Saitia, 2007). Bats' dietary richness, allied to the high diversity of niches they occupy provide valuable ecosystem services, supporting and maintaining the ecological integrity of natural and human-altered landscapes, as primary, secondary or tertiary consumers (Kunz et al., 2011). Some of the main ecosystem services provided by bats are seed dispersal (Muscarella and Fleming, 2007), pollination (Tschapka et al., 1999), and insect suppression (Cleveland et al., 2006; Kalka et al., 2008). All European bat species feed mainly on insects and other arthropods (Dietz et al., 2009). The suppression of arthropod populations is therefore the main ecosystem service that European bat species provide, resulting in the reduction of agricultural pests and leaf damage, as well as in the control of vectors of pathogens of human and other mammals (Kunz et al., 2011).

In mainland Portugal occur at least 25 bat species (ICNB, 2012), belonging to four distinct families (Miniopteridae, Molossidae, Rhinolophidae and Vespertilionidae, Figure 1.1), many of which are threatened or still remain strongly unknown (Cabral et al., 2005). All species feed mostly or exclusively on arthropods, but they have developed distinct hunting strategies, while also selecting foraging habitats and prey differently. Some of these species are "aerial-hawkers", which capture their prey during flight, while others capture their prey from substrates ("gleaners") or from water surfaces ("trawlers") (Jones and Rydell, 2003). Furthermore, some species actively search for prey while flying, while others have adopted a "sit-and-wait" strategy, detecting and hunting arthropods that fly past ("flycatchers") or move on the ground ("perch-hunters") (Jones and Rydell, 2003).

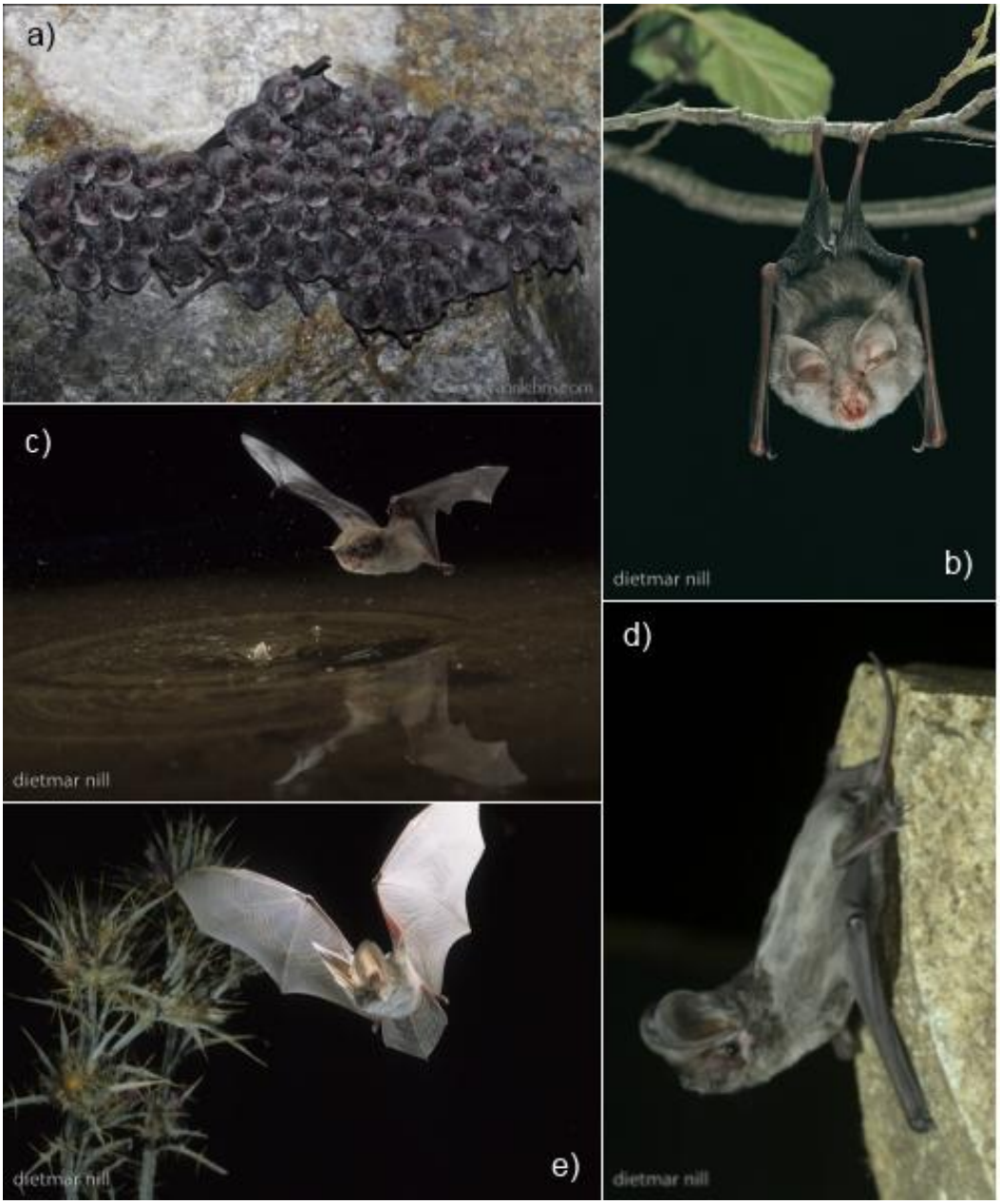

Figure 1.1 Bat species, belonging to the four families present in Portugal. a) *Miniopterus schreibersii* (Miniopteridae); b) *Rhinolophus hipposideros* (Rhinolophidae); c) *Myotis daubentonii* (Vespertilionidae); d) *Tadarida teniotis* (Molossidae); and e) *Plecotus austriacus (Vespertilionidae)*. Different hunting strategies are also represented: “aerial-hawkers”, a), b), d); “trawlers”, c); and “gleaners”, e). Photographs by Dietmar Nill and Yann LeBris (www.flickr.com), as indicated in the pictures.

1.2 IMPORTANCE OF WETLANDS FOR BATS

Wetlands are productive ecosystems that provide several resources important for human populations (Finlayson, 1999). Over centuries, humans have made various transformations in these environments, resulting from agriculture and urbanization (López-Merino et al., 2011). The increasing human population, and the consecutive growth in resource demands (e.g. food and space), has been one of the main causes for the loss and/or degradation of wetland ecosystems (Aber et al., 2012). The loss of wetlands due to intensive agriculture, mainly through drainage, besides reducing drastically the area of these relatively rare ecosystems, often results in the eutrophication of the remaining wetland areas, and in their invasion by pest (exotic or autochthonous) plant species (Zedler and Kercher, 2005). As these wetland areas are lost, so are the ecosystem services they provide, and the support of the rich biodiversity they frequently harbour (Finlayson, 1999; Zedler and Kercher, 2005).

Wetlands (Menzel et al., 2005; Lookingbill et al., 2010), as riparian habitats in general (Walsh and Harris, 1996; Grindal et al., 1999; Rainho, 2007) are recognized as important foraging habitats for bats, particularly in agriculture-based landscapes (Sirami et al., 2013), where natural remnants may be scarce. Furthermore, they may also act as commuting routes (Grindal et al., 1999; Fukui et al., 2006; Lloyd et al., 2006), enhancing landscape connectivity. Menzel et al. (2005) found that bat activity was higher in restored wetlands rather than in reference wetlands and forested areas, suggesting that wetland restoration may have immediate effects on bat populations. Similarly, Grindal et al. (1999) found higher levels of bat activity and greater capture rates in riparian habitats than in forests, along an elevation gradient, and Sirami et al. (2013) reported a significant influence of wetland size and water cover on bat activity within an agricultural matrix. This positive influence is often interpreted as a result of prey availability in these habitats. In fact, Fukui et al. (2006) found that bat activity in a riparian forest was correlated with insect abundance. These habitats may also be important to maintain bat populations in anthropogenic disturbed areas, such as production forests. The results obtained by Lloyd et al. (2006) suggest exactly that, since activity levels and bat diversity were similar among managed and unmanaged forests, within riparian buffers. However, Rainho (2007) found that water sites located within intensively managed habitats (agriculture and forestry), provide poor foraging areas. Lastly, Lookingbill et al. (2010) found that an increase in wetland network connectivity enhanced the positive association between bat activity and these environments.

1.3 BATS IN HETEROGENEOUS LANDSCAPES

There are several threats to bat populations worldwide, resulting directly or indirectly from human activities (Racey and Entwistle, 2003). Amongst them, habitat loss through transformation or degradation, and habitat fragmentation are probably the major threats to bat diversity as a whole (Primack, 2000; Avila-Flores and Fenton, 2005). One of the main reasons for such alterations is the conversion of natural habitats into agricultural landscapes. Indeed, the majority of the European territory is nowadays occupied by farmlands (Robinson and Sutherland, 2002, Billeter et al., 2008), and there are hardly any landscapes free of any type of human influence (Meeus, 1995). The conversion of natural environments into agricultural landscapes is often carried out at the expense of native biodiversity (Mickleburgh et al., 2002; Tscharntke, et al., 2005), and result in the immersion of remnant natural patches in a human-managed, agricultural matrix (Uematsu et al., 2010; Fuentes-Montemayor et al., 2013). These landscapes are usually characterized by high spatial heterogeneity, forming mosaics of crop fields and pastures, and remnant natural patches (Duchamp and Swihart, 2008). Moreover, agricultural landscapes are not stable, rapidly changing along with human activities (Di Giulio et al, 2001; DeClerck et al., 2010; Gilroy et al., 2010). Despite the known negative effects of agriculture intensification on biodiversity (Robinson and Sutherland, 2002; Tillman et al., 2002; Wickramasinghe et al., 2003; Cerezo et al., 2011), low-intensive land-use systems can actually contribute towards its conservation (Tscharntke et al., 2005).

It is thought that an increase in structural complexity of a habitat mosaic may result in greater species diversity, due to the availability of more ecological niches, and to the promotion of several distinct opportunities for resource exploitation. This is known as the "habitat heterogeneity hypothesis" (Pianka, 1966; Bazzaz, 1975; Tews et al., 2004). Within a mosaic-shaped landscape, resource availability may be spatially heterogeneous, thus its suitability to an organism may change across different regions of the landscape (Milne et al., 1989). Consequently, spatial heterogeneity may affect the dispersal patterns of organisms, as well as their foraging behaviour (Johnson et al., 1992), since the required resources may be unevenly distributed throughout the landscape patches, and the ability of an organism to exploit them may depend on the landscape connectivity. Therefore, the response given by an organism to spatial heterogeneity depends strongly on its taxonomic group, its dispersion abilities, and its perception of the surrounding habitat (Kotliar and Wiens, 1990; Malanson and Cramer, 1999; Tews et al., 2004). For instance, bat species differ in their mobility and, consequently, on their home-ranges. Therefore, the perception

of the landscape of a bat which has low mobility and a small home-range, such as *P. pygmaeus* (Nicholls and Racey, 2006), will differ completely from one of a bat with high mobility, such as *T. teniotis*, which is able to fly up to 30 km between the roost and a foraging site (Marques et al., 2004).

Although some bat species seem to have strict associations with certain habitat types, many are generalist in their use of the distinct available habitats, and often depend on multiple settings to fulfil their daily and seasonal needs especially to deal with different requirements along the various stages of their life-cycle (Law and Dickman, 1998; Lookingbill et al., 2010). Since bats are highly vagile, they can exploit the resources provided by different patches within a landscape characterized by a mosaic of habitats, and thus become less dependent on particular land cover types (Fenton 1997). Furthermore, habitat mosaics may favour the conditions necessary to the co-occurrence of different species, by allowing them to exploit different habitats (Law and Dickman 1998), and to exhibit distinct patterns of resource exploitation, even when they are morphologically similar (e.g. *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, Davidson-Watts et al. 2006).

1.4 INFLUENCE OF LANDSCAPE FEATURES ON BATS

The interaction between bats and the features of the landscape they inhabit has been the focus of several recent studies (e.g. Gorresen et al., 2005; Yates and Muzika, 2006; Perry et al., 2008; Pinto and Keitt, 2008; Klingbeil and Willig, 2009), including some that were developed in agricultural landscapes in temperate regions (e.g. Duchamp and Swihart, 2008; Popa-Lisseanu et al., 2009; Ethier and Fahrig, 2011; Fuentes-Montemayor et al., 2011, 2013; Rainho and Palmeirim, 2013).

To focus on the relationship between bats and heterogeneous landscapes, it is important to establish some definitions associated to landscape features (which will also be used during the following chapters of this study). Dunning et al. (1992) grouped the various measures of landscape structure into two general categories:

i) Landscape physiognomy, “refers to features associated with the physical layout of elements within the landscape”; and

ii) Landscape composition, refers to “the relative amounts of each habitat type contained within the landscape” and “include metrics that measure the presence, absence, or relative proportions of landscape components”.

Another important definition made by Dunning et al. (1992) was:

iii) Landscape complementation, the process that occurs when distinct patch types hold different resources both required by an organism, and they occur in close proximity within a landscape. Therefore, this landscape is able to “support a larger population than do landscapes in which these habitats are far apart”.

The majority of studies that investigated interactions between bats and landscape features revealed species- or guild-dependent responses to landscape features (e.g. Klingbeil and Willig, 2009; Fuentes-Montemayor et al., 2013; Rainho and Palmeirim, 2013), as well as different responses at different spatial scales (e.g. Gorresen et al., 2005; Perry et al., 2008). Nevertheless, in agricultural-based landscapes, a positive influence of forest cover seems to be a recurrent result (e.g. Duchamp and Swihart; 2008; Fuentes-Montemayor et al., 2011). Within a heterogeneous matrix dominated by agricultural lands, interspersed with remnant forest patches, Ethier and Fahrig (2011) found a positive influence of fragmentation on bat abundance, and showed that landscape complementation is the main mechanism supporting that relationship. On the contrary, the results obtained by Popa-Lisseanu et al. (2009) showed a negative influence of habitat fragmentation on the populations of *Nyctalus lasiopterus*. The authors justified this negative effect as a result of the large distances between adequate roosting and foraging habitats, which can be interpreted as low landscape complementation, following the definition provided by Dunning et al. (1992).

The abovementioned studies have already provided some knowledge on the interaction between bats and landscape features in heterogeneous environments. However, there are still important gaps concerning the patterns of bat occurrence within those landscapes and of the processes behind them.

1.5 OBJECTIVES

The Baixo Vouga Lagunar, located in the Central-North Portuguese coast, is an area characterized by a human-altered heterogeneous landscape, composed by a complex matrix of natural, semi-natural and human-made habitats. In close contact with an estuarine coastal lagoon, this region detains unique features, and is regarded as holder of a rich biodiversity. However, little is known about the spatial and temporal patterns of vertebrate distribution, particularly regarding bats.

We hypothesise that:

1. Bat assemblages structure and composition varies among the habitat types occurring in the area;
2. Species differing in morphology and hunting strategies vary in their habitat preferences within the region;
3. The activity levels of the co-occurring bat species are limited by seasonality;
4. Bat activity and richness are explained by both landscape and local features within the study area;
5. The response given by bat activity to landscape characteristics varies across a gradient of focal scales; and
6. Different bat guilds respond differently to landscape and local features.

With this study, we expect to obtained important knowledge on several aspects of bat ecology, leading to a better understanding about the interaction between these animals and the heterogeneous landscape of BVL. Hopefully, the knowledge acquired with this study will be interpreted as a solid base for future research, conservation plans and land management decisions, and help in the interpretation of the relationship between bats and human-altered, heterogeneous landscapes elsewhere.

1.6 FRAMEWORK

The present study is included in a broader project named “Factors that affect the seasonal and spatial patterns of vertebrate diversity and activity in different habitat types of the humanized landscape of Baixo Vouga Lagunar”, developed by a team of MSc students,

under the scientific orientation of PhD and Postdoctoral researchers of the Wildlife Research Unit, Department of Biology, Centre for Environmental and Marine Studies, University of Aveiro (Figure 1.2). This project arises from the need to understand the spatial and seasonal patterns of the distribution of species that occur in the humanized landscape of BVL, as well as to determine which are the factors influencing them.

This region, holder of a great biological diversity, is characterized by a mosaic landscape, with aquatic and terrestrial environments, and a great habitat diversity, largely shaped by the secular human action (Brito et al., 2010). However, knowledge about the dynamics of the animal populations, assemblages and communities that occur in the region is still very scarce.

Figure 1.2 Satellite image of the region, institutions responsible for co-funding of the project (Municipality of Estarreja[1] and Observatoires Hommes-Millieux[2]) and institutions involved in the BVL project located in Estarreja (BioRia[3]) and Aveiro (University of Aveiro – Department of Biology[4], CESAM[5], and Wildlife Research Unit[6]).

[1] http://www.cm-estarreja.pt/
[2] http://www.ohm-inee.cnrs.fr/
[3] http://www.bioria.com/
[4] http://www.ua.pt/dbio/
[5] http://www.cesam.ua.pt/
[6] https://sites.google.com/site/unidadevidaselvagem/

This project intends to bridge this gap in the scientific knowledge, by investigating a patterns and processes of diversity and abundance of a wide variety of vertebrate and invertebrate *taxa*, belonging to several trophic levels, namely insects, amphibians, small non-volant mammals, bats, carnivores and birds.

The scheduling of the several fieldwork components, relative to the different studied taxonomic groups, took into account an optimization effort regarding human, material and financial resources, through the mutual help of the team members.

The main objectives of the project, transversal to all the studies are:

1) To detect spatial patterns of diversity within the mosaic of habitats of the region;
2) To assess the existence of seasonal patterns in the occupation of the different habitats, by the various taxa under study;
3) To identify the main factors behind those patterns, relating species presence with biotic, abiotic and anthropogenic variables;

Based on the scientific knowledge already acquired and to be acquired in the future, and by the means of ecological modelling approaches, the elaboration of maps of priority conservation and management areas is also intended. This will allow the proposal of very specific management actions.

This project will be used as groundwork for future ecological research in the BVL area by the Wildlife Research Unit team, as well as to a more sustainable exploration and management of its natural resources, by giving continuity to established partnerships (e.g. Municipality of Estarreja) and searching for new ones with the local stakeholders.

Three other MSc theses resulted from this project. The specific goals and main results obtained in each one are as follows:

"*Factors affecting the diversity of amphibians in Baixo Vouga Lagunar*"

Globally, the main objectives of this study, developed by Inês Torres, were to understand which factors determine the distribution and diversity of amphibians within the heterogeneous landscape of Baixo Vouga Lagunar. The sampling of amphibians was done in three replicates of seven habitat types representative of the study area: *Bocage*, rice fields, maize fields, marshland, reed beds, sea rushes and forest. Several methodologies were applied simultaneously, and in a standardised way. Additionally, prey abundance was assessed by using light traps to sample insects. 12 different species of

amphibians were identified, corresponding to approximately 70% of the species occurring in Portugal. Preliminary results indicate that prey availability is one of the most important factors behind the community composition of these animals. Furthermore, the distance to wells was found to be the best predictor for amphibians richness, underlining the importance of those structures within an agriculture-dominated landscape such as Baixo Vouga Lagunar.

"Foraging and spatial ecology of Marsh harrier in Baixo Vouga Lagunar"

The study of the bird of prey *Circus aeruginosus*, developed by Michelle Alves, aimed to investigate the species preferences of habitats and prey, as well as the factors that determine its occurrence and abundance. Sampling was conducted through direct observation of the individuals, in fixed points within the study area, in a daily sampling throughout an annual cycle. Regurgitations and prey remaining were collected, so the diet of the species could be assessed. The results obtained revealed a diverse diet that included small mammals, birds, reptiles, insects and eggs. However, a clear preference and selection towards *Microtus* sp. was found. Besides prey availability, natural habitats such as reed beds and marshlands were found to be positively associated with species presence and abundance. within the Baixo Vouga Lagunar landscape.

"Mammal choices in the heterogeneous landscape of Baixo Vouga Lagunar"

The study of the terrestrial non-volant mammals, developed by Sara Marques, addresses the predator-prey interaction, being use several different methodologies for the investigation of small mammals and carnivores. The inventory of the small mammals community in the BVL, and the analysis of its spatial and temporal distribution across the different sampled habitat types, representative of the study area (rice field, Bocage, reed bed, forest, sea rush, maize field and marshland) was based on the capture-mark-recapture methodology, involving the use of Sherman traps. An analysis of the spatial distribution of mammals over the whole area was done, taking in consideration the habitat type. For that, two non-invasive methods were used: sign surveys and camera-trapping (using Bushnell^{TM} Trophy XLT cameras with motion sensor). The main results obtained revealed a negative influence of exotic forests on terrestrial mammals, and positive associations between small mammals and wetland habitats, and between carnivore richness and freshwater courses (i.e. riparian habitats). Lastly, heterogeneity seemed to

positively influence small mammal fauna at the landscape-scale, and together with fragmentation, to negatively influence carnivore richness. Riparian habitats can therefore be regarded as some of the most important habitats for terrestrial mammals within the heterogeneous landscape of Baixo Vouga Lagunar.

1.7 THESIS STRUCTURE

This thesis is organized in five main chapters. In the first chapter we present a general introduction, as well as the framework of this study and its main objectives. In the second chapter we provide a description of the study area. In the following chapters we present the main research questions and findings. These are presented in two distinct scientific papers. The first entitled “A mosaic of opportunities? Spatio-temporal patterns of bat diversity and activity in a strongly humanized Mediterranean wetland” (chapter 3), focuses objectives 1 to 3, and the second entitled “Bat richness and activity in heterogeneous landscapes: guild-specific and scale-dependent?” (chapter 4) focuses objectives 4 to 6.

The main findings of this study are provided in chapter five, as well as some general conclusions, implications for bat conservation, and suggestions for future research. Lastly, the literature cited is provided in chapter 6.

Chapter 2

STUDY AREA

2. STUDY AREA

2.1 LOCATION

The study area is located in the Aveiro district (40º39-52'N, 8º27-45'W), on the Central-North Portuguese coast. In order to complete the objectives in this study, two different study area sizes were defined. For the objectives proposed on chapter 3, we defined a study area of approximately 15,000 ha, considerably smaller than the one defined for chapter 4, of approximately 50,000 ha. This difference is due to the landscape analysis performed on chapter 4, which increased greatly the proportion of the landscape to be analysed. At the wider perspective, it involves the municipalities of Albergaria-a-Velha, Aveiro, Estarreja, Ílhavo, Murtosa, Oliveira de Azeméis and Ovar (Figure 2.1). The study area encompasses a subregion known as Baixo Vouga Lagunar (BVL), as well as its surroundings. However, for simplifying purposes, the study area will be hereafter referred simply as BVL.

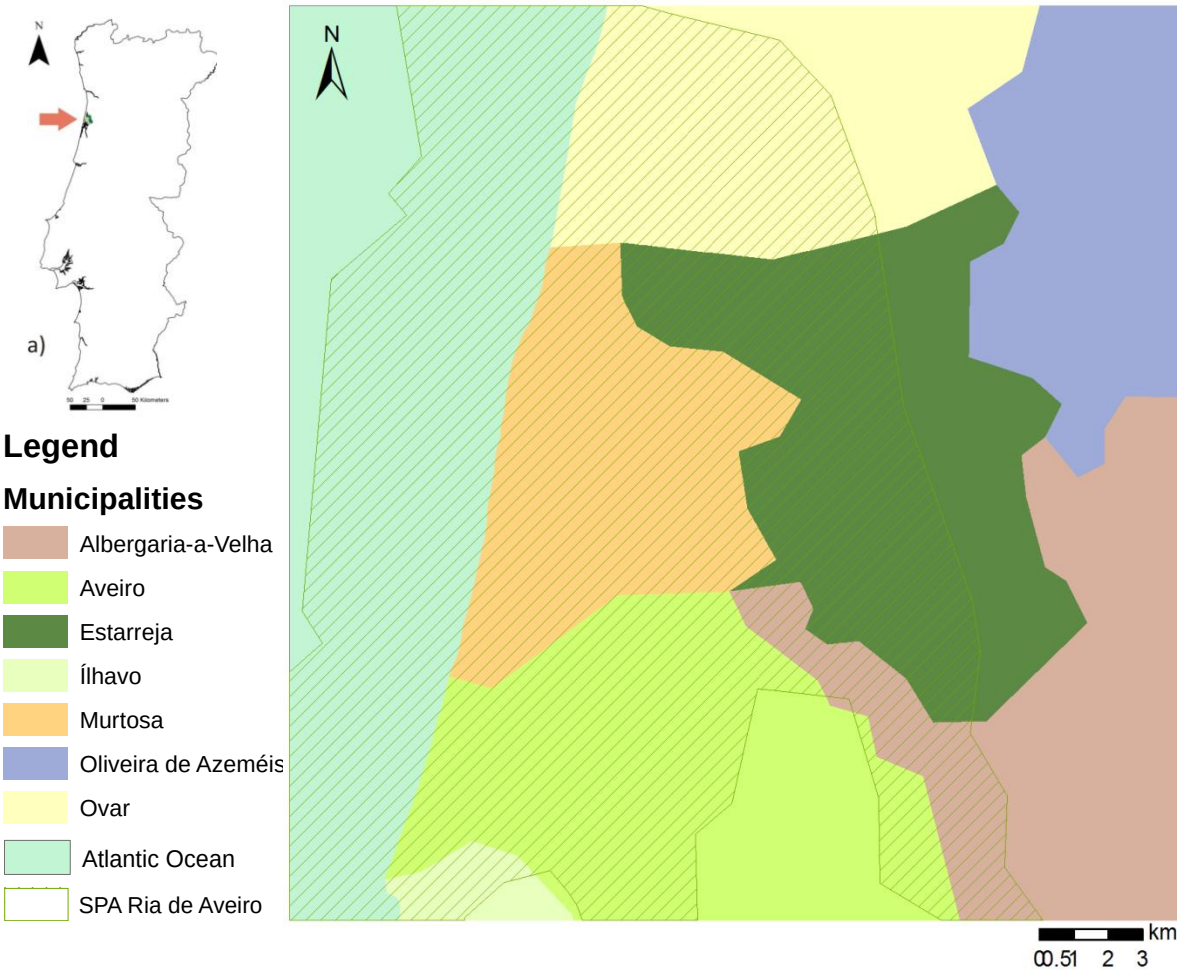

Figure 2.1 a) Location of the study area in mainland Portugal; b) Municipalities encompassed, and limit of the Ria de Aveiro special protection area (ZPE). Adapted from "Atlas do Ambiente Digital" (APA, 1998).

2.2 CHARACTERIZATION

The BVL subregion harbours a rich biodiversity (Brito et al., 2010). Furthermore, a great proportion of the study area is classified as a special protection area (SPA) of the Ria de Aveiro coastal lagoon (Figure 2.1), under the Birds Directive (79/409/EEC).

The landscape is characterized by a heterogeneous landscape, with a mosaic of natural, semi-natural and human-altered habitats, including aquatic and terrestrial environments (Figure 2.2). As a coastal wetland, it presents several characteristic habitats such as marshlands, low-lying lands functioning as a transition between saltwater and terrestrial habitats, mainly dominated by *Spartina maritima*, *Salicornia ramosissima*, *Sarcocornia*

perennis and *Halimione portucaloides*; sea rushes, also a transition habitat between aquatic and terrestrial environments, characterized by large extensions of *Juncus maritimus*; and reed beds, wetlands where the influence of saline water is limited, characterized by large extensions of *Phragmites australis*. This region is strongly humanized, and agricultural land occupies a great proportion of the landscape (Table 2.1). The most frequent crops are those of maize (*Zea mays*), which are temporary crop fields, managed somehow intensively, which are distributed throughout almost all of the landscape. Distributed in a much more restricted way, and occupying only a small proportion of the landscape, are the rice fields. These are temporarily flooded crop fields dedicated to the culture of *Oryza sativa*. A traditional form of agriculture is also present, the *Bocage*. This unique man-made habitat, is characterized by small areas of crops and pastures, intersected by small freshwater courses and live fences of autochthonous trees (e.g. *Alnus glutinosa, Salix atrocinerea, Quercus robur*), shrub and herb hedgerows (e.g. *Hedera* spp., *Rubus* spp.). In Portugal, this type of agricultural practice is limited to the BVL region, and otherwise in Europe only to southern France and northern England (Brito et al., 2010). Woodlands within the BVL landscape are fragmented, and mostly composed by production, non-deciduous tree species, mainly by the exotic *Eucalyptus globulus*, but also *Pinus pinaster*. Several localities, mostly villages, as well as numerous industries can also be found both within and in the outskirts of BVL.

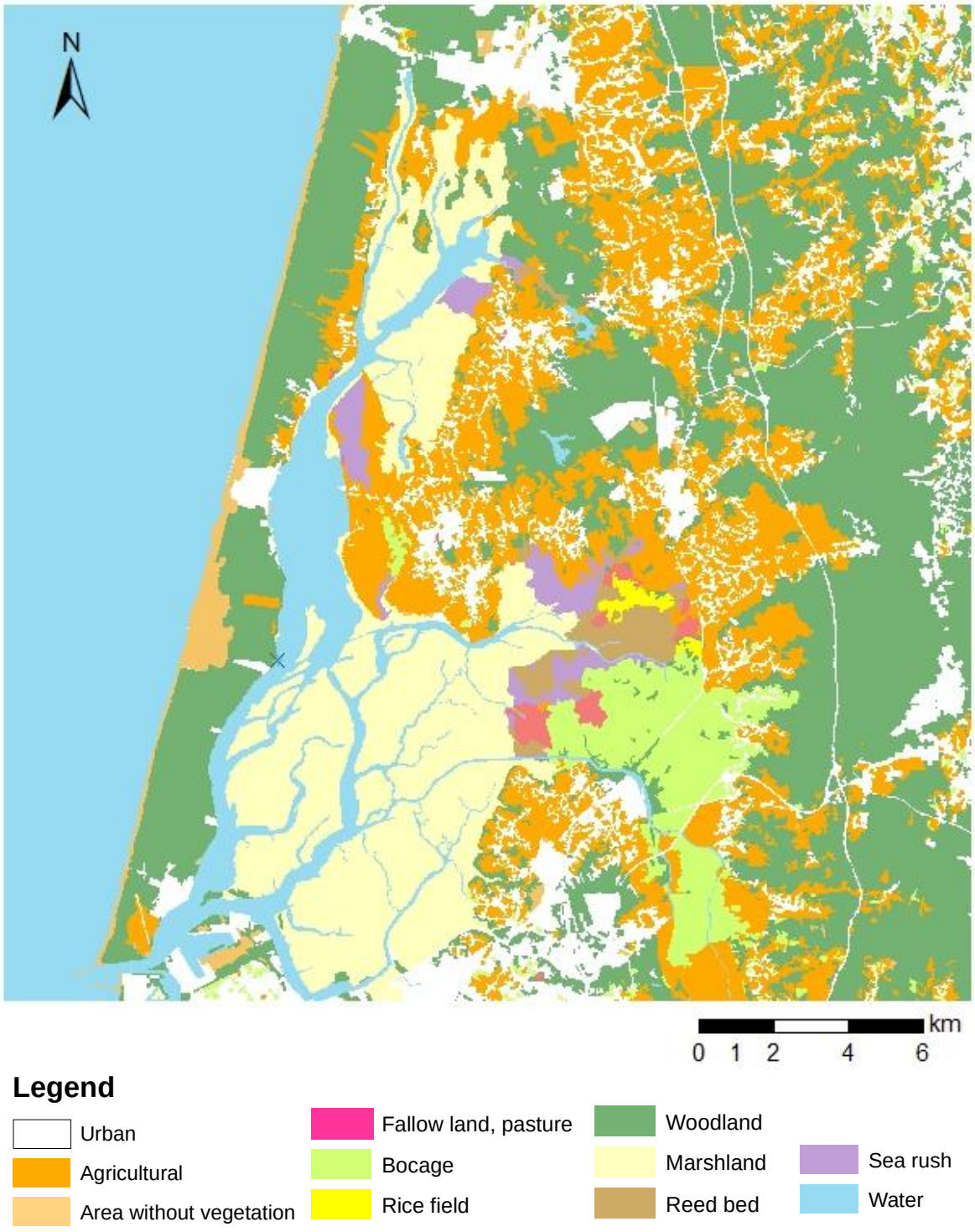

Figure 2.2 Main land cover classes in the study area. Adapted from "COS' 2007" (IGP, 2010).

Table 2.1 Area and percentage of landscape of each land cover class, for study area I (used in chapter 3) and II (used in chapter 4).

Land cover class	Study area I		Study area II	
	Area (ha)	Percentage (%)	Area (ha)	Percentage (%)
Urban	1686.75	12.84	7,676.10	14.07
Agricultural	4147.22	31.58	15,796.49	28.95
Fallow land, pasture	291.26	2.22	291.26	0.53
Bocage	944.85	7.19	2,186.16	4.00
Rice field	119.30	0.91	119.30	0.22
Woodland	2159.81	16.45	15,764.20	28.90
Marshland	2176.90	16.58	9,111.64	16.70
Reed bed	549.51	4.18	579.20	1.06
Sea rush	813.97	6.20	813.97	1.49
Area without vegetation	242.74	1.85	2,218.12	4.07

2.3 CLIMATE

The BVL region is a transition zone between Atlantic and Mediterranean climates, with a strong influence of the Atlantic Ocean (Costa et al., 1998; Bonmati et al., 2006). During the study period (October 2011 – September 2012), mean air temperature was 14.5 ºC (oscillating between 8.5 ºC in February and 19.8 ºC in September), and mean annual humidity of 76.5% (data from CUF weather station). Accumulated precipitation varied between 5.6 mm in July and 194 mm in November, with an annual value of 627.6 mm (data from CESAMET).

Chapter 3

A MOSAIC OF OPPORTUNITIES? SPATIO-TEMPORAL PATTERNS OF BAT DIVERSITY AND ACTIVITY IN A STRONGLY HUMANIZED MEDITERRANEAN WETLAND

3. A MOSAIC OF OPPORTUNITIES? SPATIO-TEMPORAL PATTERNS OF BAT DIVERSITY AND ACTIVITY IN A STRONGLY HUMANIZED MEDITERRANEAN WETLAND

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3.1. ABSTRACT

We investigated the spatial and seasonal patterns of bat diversity and activity in the heterogeneous landscape of Baixo Vouga Lagunar, Portugal. We acoustically sampled bats across 24 sampling sites representative of the six main habitat types that shape the landscape. We compared bat diversity, evenness and richness across habitat types and seasons, and analysed the spatial and seasonal patterns of overall bat activity, as well as of individual species and guilds. From the total of 1544 bat passes recorded, we identified twelve different species. *Pipistrellus pygmaeus*, *Pipistrellus pipistrellus* and *Eptesicus serotinus*/*Eptesicus isabellinus* stood out as the most frequently recorded. We found bat assemblages of the different habitats to be relatively similar, and that bat activity hardly differed between the habitats studied. However, we found seasonal differences in bat activity within habitats. Overall, our results indicate that bats exploit all habitats of this heterogeneous area, and that the mosaic landscape provides them several opportunities, which results in strong seasonal and spatial dynamics.

3.2 INTRODUCTION

Anthropogenic disturbances, particularly those that reduce, fragment and transform natural habitats, constitute some of the main threats to biodiversity worldwide (Primack, 2000; Avila-Flores and Fenton, 2005). However, human-dominated landscapes harbour much of the world's biodiversity (Dixon, 2012), and have been the main focus of several studies in recent years (e.g. Wickramasinghe et al., 2003; Johnson et al., 2008; Miller et al., 2009).

Due to the growing demands of a rapidly increasing human population, several natural ecosystems have been converted to agricultural landscapes (Robinson and Sutherland, 2002; Kunz et al., 2011), often at the expense of biodiversity (Mickleburgh et al., 2002; Uematsu et al., 2010). These landscapes are usually characterized by high spatial heterogeneity; forming mosaics of crop fields, pastures and remnant natural patches (Duchamp and Swihart, 2008). Furthermore, agricultural landscapes are not stable, since they change rapidly in concert with human activities (Di Giulio et al., 2001; DeClerck et al., 2010; Gilroy et al., 2010). The intensification of farming (Wickramasinghe et al., 2003), along with loss of landscape elements such as hedgerows and boundaries (Tscharntke et al., 2005; Mehr et al., 2011), increasing use of pesticides (Canova and Fasola, 1991; Jones et al., 2009), and land abandonment (Rainho et al., 2010), are known to be some of the main threats to several animal groups that occur in these strongly human-dominated landscapes.

Despite the growing efforts towards the conservation of foraging habitats of threatened species within agricultural landscapes in Europe (Rainho and Palmeirim, 2011), multidisciplinary approaches combining land owners, researchers and law makers are still needed to create adequate conservation and management plans for these areas (Pimentel et al., 1992; Ornerod et al., 2003). Knowledge about the responses of fauna and flora to habitat transformation is therefore a key issue in the conservation of species that occur within heterogeneous landscapes (Uematsu et al., 2010; López-Arévalo et al., 2011). However, understanding and predicting the mechanisms behind those responses still present a major challenge for biologists (Bernard and Fenton, 2007).

Bats form an incredibly diverse group both taxonomically (with about 1300 species presently described, Kunz et al., 2011) and ecologically, with several distinct life-histories, behavioural patterns and feeding and roosting habits (Patterson et al., 2003; Simmons and Conway, 2003). The dietary richness of bats (as primary, secondary or tertiary

consumers) makes them extremely valuable to ecosystems, as they play a key role in supporting both natural and human-dominated landscapes (Lumsden and Bennett, 2005; Muscarella and Fleming, 2007; Kunz et al., 2011; Jung et al., 2012). All European bat species feed mainly on insects and other arthropods (Dietz et al., 2009). Therefore, the main ecosystem service that European bat species provide is the suppression of arthropod populations, resulting in the reduction of agricultural pests and leaf damage, as well as in the control of vectors of pathogens of humans and other mammals (Kunz et al., 2011). Furthermore, bats are also very good bioindicators and are used for assessing habitat quality, as well as for interpreting the effects of human-induced changes on ecosystems (Wicramasinghe et al., 2003; Jones et al., 2009; but see Cunto and Bernard, 2012). Indeed, the rapid ecosystem changes caused by humans, such as fragmentation or destruction of roosting and foraging habitats, have been linked to the decline and isolation of bat populations all over the world (Jones et al., 2003; Akasaka et al., 2009).

In spite of being relatively stable within a given landscape, species composition varies amongst the several habitat types that shape that landscape (Moreno and Halffter, 2001; Ramos Pereira et al., 2009; Avila-Cabadilla et al., 2012). These differences in species distribution may reflect a preference for some habitats relative to others according to a species sorting patch dynamics model (see Leibold et al., 2004; Cottenie, 2005; Holyoak et al., 2005 for reviews of patch dynamics models).

Therefore, knowledge about habitat use by bats, including foraging and roosting habitats, should be one of the main foundations on which conservation and land management decisions are made (Stebbings, 1988; Walsh and Harris, 1996).

Bats seem to select habitats on the basis of a series of hierarchical decisions, both at landscape and local scales (Ford et al., 2006). At landscape scale, bat habitat use is mainly dictated by day-roost availability, proximity to winter hibernacula and foraging sites, presence of water sources, climate conditions and human-induced disturbances (Furlonger et al., 1987; Gehrt and Chelsvig, 2003; Evelyn et al., 2004; Ford et al., 2006; Johnson et al., 2008, Rainho et al., 2010), while at the local scale, site selection is often influenced by proximity to riparian habitats, vegetation structure, morphological and echolocation characteristics, and prey preferences (Aldridge and Rautenbach, 1987; Ford et al., 2005, 2006; Johnson et al., 2008). Thus, habitat selection is a species-specific process, often reflecting species' morphological characters, as well as their foraging strategies and echolocation call structures (Kalko and Schnitzler, 1993; Lundy and Montgomery, 2010). While some species are generalist users of habitats, others seem to

have strict associations with specific habitat types. Together with their ecological diversity and flexibility, the high mobility of bats (enabled by their ability to fly rather long distances at relatively low energetic costs) often makes their species-habitat associations difficult to assess. This seems to be particularly true when the landscape matrix is characterized by a mosaic of habitats, allowing bats to explore different sites and to become less dependent on a particular setting (Fenton, 1997). However, habitat mosaics may favour the conditions necessary to allow co-occurring species to feed in different habitats (Law and Dickman, 1998), and to exhibit distinct patterns of resource exploitation, even when they are morphologically similar (e.g. *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, Davidson-Watts et al., 2006). Therefore, the analysis of these spatial patterns of co-existing species may provide important information about the mechanisms of resource selection and partitioning between species (Aguiar and Marinho-Filho, 2004).

The activity of insectivorous bats in temperate regions is strongly limited by the cold winter temperatures and the consequent food shortages (Kapfer and Aron, 2007). Furthermore, bat flight and foraging activity often reveal daily and seasonal variations, reflecting changes in insect availability (Bartonicka and Zukal, 2003) and weather conditions, which can directly or indirectly influence bat activity (Meyer et al., 2004).

In this study, we aim to investigate seasonal and spatial patterns of bat diversity and activity in the Baixo Vouga Lagunar area, Central-West Portugal. Here, the landscape is characterized by a matrix of natural wetland formations (from fresh to brackish water), interspersed by intensive and extensive agricultural fields, pastures and production forests. Specifically, our objectives are: 1) to identify and characterize the bat assemblages of the main habitat types occurring in the area; 2) to assess how different species differing in morphology and hunting strategies vary in their habitat preferences within the region, and 3) to examine the seasonal activity patterns of the co-occurring bat species.

3.2. MATERIALS AND METHODS

Study Area

The study area (Figure 3.1) is located in the Aveiro district (40º39-50'N, 8º30-42'W) on the northern Portuguese coast. It has an area of approximately 15,000 ha and encompasses a region known as Baixo Vouga Lagunar (BVL). Hereafter, we refer to our study area as BVL, although it also encompasses the surrounding areas of that region. It is limited to the South by the Vouga River estuary and to the West by an estuarine coastal lagoon, Ria de Aveiro. The landscape reflects an ecotone between water- and land-based habitats, harbouring several characteristic habitats such as marshlands, reed beds and sea rushes. The region is strongly humanized, with many agricultural fields, forest monocultures and urbanizations. Eight different types of habitat were distinguished within the study area:

I. *Bocage*: this unique habitat is characterized by small areas of crops and pastures, surrounded by live fences of autochthonous trees (e.g. *Alnus glutinosa, Salix atrocinerea, Quercus robur*), shrub and herb hedgerows (e.g. *Hedera* spp., *Rubus* spp.) and small freshwater courses. The distribution of *Bocage* in Portugal is limited to the BVL region and, besides this area, it only occurs in southern France and northern England (Brito et al., 2010);

II. Forest: includes woodland patches mainly of *Eucalyptus globulus* and *Pinus pinaster* monocultures;

III. Maize fields: these are temporary crop fields mainly dominated by maize *(Zea mays*) cultures;

IV. Marshland: low-lying lands functioning as a transition between saltwater and terrestrial habitats. The vegetation is mainly dominated by *Spartina maritima*, *Salicornia ramosissima*, *Sarcocornia perennis* and *Halimione portucaloides*;

V. Reed beds: these are wetlands where the influence of saline water is limited, characterized by large extensions of *Phragmites australis*;

VI. Rice fields: these are temporarily flooded crop fields dedicated to rice culture (*Oryza* sp.);

VII. Sea rushes: transition habitat between aquatic and land habitats, characterized by large extensions of *Juncus maritimus*;

VIII. Urban: human settlements, with artificial lighting and asphalt roads.

The area is characterized by a temperate climate with a strong Atlantic influence, with well-defined seasonal variation both in air temperature (registered mean annual temperature of 14.5 ºC, with an amplitude between 8.5 ºC in February and 19.8 ºC in September), and rainfall (registered annual precipitation of 627.6 mm, varying between 5.6 mm in July and 194 mm in November). BVL is also characterized by high humidity throughout the year (mean annual humidity of 76.5%) (air temperature and humidity data from CUF weather station, and precipitation from CESAMET, all relative to the October'11-September'12 period).

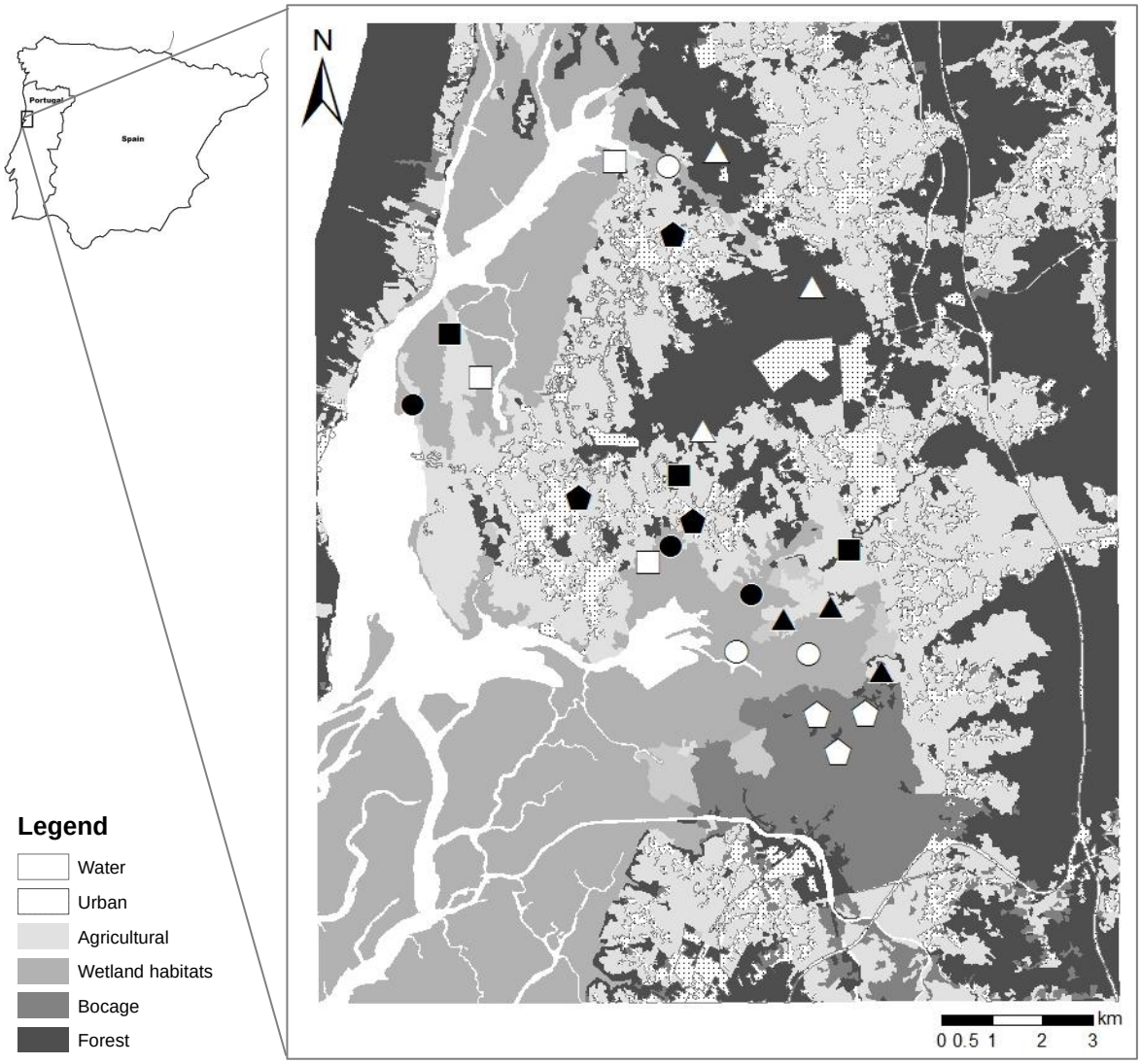

Figure 3.1 Approximate location of the study area in the Iberian Peninsula, main land use characterization and location of the sampling sites. Sampling sites divided in maize field (black squares), rice field (black triangles), sea rush (black circles), urban (black pentagons), marshland (white squares), forest (white triangles), reed bed (white circles) and *Bocage* (white pentagons).

Bat activity

Bat activity was sampled through acoustic monitoring. Acoustic sampling was done in three replicates of each habitat type, at a total of 24 sites. Sites were chosen at a minimum intervening distance of 1 km to reduce spatial autocorrelation. Since variation between nights and sites can be significant (Broders, 2003; Wickramasinghe et al., 2003; Ford et al., 2005), each site was sampled twice a month, between October 2011 and September 2012, except during the months of April and July when the weather conditions only allowed each site to be sampled once. No sampling was carried out on nights with unfavourable weather conditions such as rain or strong winds, since bat activity (Ford et al., 2005, 2006) and detectability (Dixon, 2012) are negatively affected by these conditions. Acoustic sampling was done within the first 2.5h-3h after dusk, when bat activity levels are highest (Rydell et al., 1996; Hayes, 1997). The nightly order of site visitation was chosen randomly, so that data bias could be avoided.

For each site, a 15-minute walking survey was carried out using a Pettersson D240x ultra-sound detector (Pettersson Elektronik AB™, Uppsala, Sweden) in heterodyne mode, rapidly travelling through the full range of frequencies so that the chance of detecting different bat species was maximized (Russ and Montgomery, 2002). Sample calls of 1.7 seconds were recorded in time expansion mode into a digital recorder (Edirol R-09, Roland Corp., Shizuoka, Japan). Walking surveys were carried out at a regular pace so that all transects were approximately 500 m in length.

Bat calls were analysed using Audacity 1.3.13 software (http://audacity.sourceforge.net). Call duration, inter-pulse interval, start and end frequencies and peak frequency (frequency containing most energy) were registered. Species identification was done using a reference collection of bat calls and dichotomous keys for Portuguese and Iberian bat species (Lisón, 2011; Rainho et al., 2011). When two species could not be distinguished by their echolocation calls, they were grouped into two-species complexes, as shown in Table 3.1.

Three types of calls were discriminated: (1) echolocation passes, defined as a sequence of echolocation pulses emitted by bats while navigating and searching for food (Lookingbill et al., 2010), (2) feeding buzzes, characterized by an approach phase with progressively lower signal duration and pulse interval, ending in a series of short signals with high repetition rate (Schnitzler and Kalko, 2001), and (3) social calls, defined as broadband

calls of longer duration than echolocation calls, with multiple low-frequency components (Altringham and Fenton 2009).

Statistical analysis

Patterns of species richness, diversity and composition

We calculated three indices within the eight main habitat types that compose the BVL landscape: diversity, evenness and species richness. Since most diversity indices employed actually refer to entropies rather than true diversities (Keylock, 2005; Jost, 2006), we used a conversion of the Shannon-Wiener index (H) on its "numbers equivalent" as a measure of diversity, as proposed by Jost (2006). Hereafter, this diversity measure is simply referred to as diversity (D). We also used a modified Pielou's evenness – hereafter, termed evenness (E) – that was calculated using D instead of H. We then performed generalized linear models (GLM) and Tukey post-hoc multiple comparisons for each index to assess differences between seasons and habitat types. In addition, we performed an analysis of similarities (ANOSIM) to evaluate the significance of the differences between the species composition of the studied habitats.

Activity of species and guilds

Several methods have been used in the literature to measure bat activity, such as counting the absolute numbers of search-phase echolocation calls (Avila-Flores and Fenton, 2005), counting the number of minutes in which bats are registered (McAney and Fariley, 1988), calculating the mean number of passes per night for each sampling site (Gehrt and Chelsvig, 2003), summing the number of one-minute periods in which a species was recorded (Activity Index; Miller, 2001) or the sizes of files recorded in a specific space and time unit (Broders, 2003). However, despite this variety, none of the above methods discriminate between passes of commuting bats and passes actually made by bats foraging in the sampled site (Carmel and Safriel, 1998). For this reason, and to overcome differences in sampling effort, we estimated bat activity using the number of bat passes per 15 minute interval (i.e. the number of passes per transect).

For the seven species with more than 10 recorded passes (Table 3.1), we performed a hierarchical clustering analysis based on percentage of habitat use and assessed species-specific temporal and spatial patterns of activity.

To test for overall bat activity, feeding activity and social behaviour dependence on habitat type and seasonality, we performed generalized linear mixed models (GLMM) on overall bat passes, feeding buzzes and social calls. We then carried out Tukey post-hoc multiple comparisons for each model to detect which habitats and seasons were significantly distinct. To evaluate differences in bat activity between habitats in each season, we performed GLMM on overall bat passes, followed by multiple comparisons. We also carried out GLMM to test for species activity dependence on habitat type and seasonality, together with multiple comparisons for each model to assess differences between habitats and seasons. Because species with low intensity or very high frequency calls may be underrepresented (Ciechanowski, 2002; Hayes et al., 2009), no comparisons between activity levels of different species were made. Since echolocation-monitoring studies are unable to provide a true count of individuals (Hayes et al., 2009), the data was not interpreted as a measure of abundance, but rather as an estimate of bat activity. This enables the comparison of relative use between different habitat types and of the variation in habitat use over time (Hayes, 2000).

We divided bat species into three guilds based on eco-morphological traits (Fenton, 1990; Schnitzler and Kalko, 2001). Species that have a fast and energetically inexpensive flight type, with high wing loading and aspect ratio, and emit long, narrowband and low-frequency calls, were considered as “open-space foragers”. Species that present a slow and energetically inexpensive flight type, with average wing loading and aspect ratio, and echolocate through short pulses that are often composed of both broad and narrowband components, were considered as “edge foragers”. Lastly, species with low wing loading and aspect ratio, i.e. energetically expensive but very manoeuvrable flight, and whose echolocation is characterized by low-intensity, broadband calls, were considered as “closed-habitat foragers”. The species within each guild are presented in Table 3.1. Since we only recorded *P. auritus*/*P. austriacus* (the only closed-habitat species recorded) on one occasion, this guild was not included in the analysis. For the other two guilds, we performed GLMM and multiple comparisons, to assess differences in bat activity between habitat types and seasons. Calls identified to genus level or to species-complexes were included in this analysis whenever the group of potential species all belonged to the same guild.

ANOSIM was performed with Past software, version 2.17c (Hammer et al., 2001); all the remaining statistical analysis were performed with software R, version 2.15.1 (R Core Team, 2013). The level of significance was established at $p \leq 0.05$, although we also report and discuss near significant probability values at $p < 0.1$.

3.3. RESULTS

Spatial patterns of species richness, diversity and composition

Of the total of 1544 bat passes recorded during this study, we identified 1262 (82%) to species level (Table 3.1). The identified species (or two-species complexes) were *Barbastella barbastellus*, *Eptesicus serotinus*/*E. isabellinus*, *Myotis daubentonii*, *M. escalerai*, *M. myotis*/*M. blythii*, *Nyctalus lasiopterus*/*N. noctula*, *N. leisleri*, *Pipistrellus kuhlii*, *P. pipistrellus*, *P. pygmaeus*, *Plecotus auritus*/*P. austriacus* and *Tadarida teniotis*. The remaining recordings were classified as *Eptesicus* spp./*Nyctalus* spp.(13), *Myotis* spp. (13), *Nyctalus* spp. (26), *Pipistrellus* spp. (154) and unidentified calls (76).

P. pygmaeus, *P. pipistrellus* and *E. serotinus*/*E. isabellinus* stood out as the most frequently recorded species, comprising a total of 91.2% of the calls identified to species level. These three species, along with *N. lasiopterus*/*N. noctula*, were recorded in all habitat types. Of the 12 identified species, five were rarely recorded (*B. barbastellus*, *M. daubentonii*, *M. escalerai*, *P. kuhlii* and *P. auritus*/*P. austriacus*), with less than 10 bat-passes each.

We found no significant differences in diversity, evenness and species richness between habitat types. Mean values of diversity, evenness and richness for all habitats and seasons are presented in Table 3.2. Species composition analysis, assessed through a one-way ANOSIM, revealed marginally non-significant differences between bat assemblages among the different habitat types ($R=0.15$; $p=0.06$).

Spatial patterns of bat activity

Cluster analysis of the percentage of total activity per habitat type for the seven species with more than 10 recorded passes (Figure 3.2) revealed three main clusters; one grouping the edge-forager *M. myotis*/*M. blythii* and the open-space forager *N. leisleri*, a second one constituted only by *T. teniotis*, and a third one grouping *P. pipistrellus*, *P. pygmaeus*, *E. serotinus*/*E. isabellinus* and *N. lasiopterus*/ *N. noctula*.

A high percentage of the total activity of *M. myotis*/*M. blythii* and *N. leisleri* occurred in forests (40.0 and 38.5%, respectively) and reed beds (20.0 and 26.9%, respectively). *T.*

teniotis showed highest activity in uncluttered habitats (82.4% in rice fields, sea rushes and reed beds) and it was separated from another cluster containing the genera *Pipistrellus*, *Nyctalus* and *Eptesicus* that occurred in all habitat types. Within this latter cluster of more generalist species in terms of habitat use, two sub-clusters were formed, which separated the *Pipistrellus spp.* from *E. serotinus*/*E. isabellinus* and *N. lasiopterus*/*N. noctula*. Both *P. pipistrellus* and *P. pygmaeus* exhibited a high percentage of activity at urban sites (26.5 and 26.9%, respectively) and low activity in forest sites (only 5.3 and 6.4%, respectively). Conversely, *E. serotinus*/*E. isabellinus* and *N. lasiopterus*/*N. noctula* presented higher levels of activity in forest sites (28.4 and 16.7%, respectively) and lower values at human settlements (17.2 and 8.3%, respectively) compared to *Pipistrellus* species.

GLMM and multiple comparisons revealed little influence of habitat type on overall bat activity, only showing that urban settings presented significantly more activity than marshlands (z=3.03; p=0.05).

Table 3.1 List of species recorded, and respective conservation status in Portugal (Cabral et al., 2005), and worldwide (IUCN, 2013). Total number of bat passes (BP), feeding buzzes (FB), social calls (SC), and number of bat passes recorded in each habitat type. Habitat types abbreviations as: *Bocage* (Boc), forest (For), maize field (Mai), marshland (Mar), reed bed (Ree), rice field (Ric), sea rush (Rus) and urban (urb).

Species	Status		BP	FB	SC	Bat passes per habitat type							
	PT	IUCN				Boc	For	Mai	Mar	Ree	Ric	Rus	Urb
Closed-habitat foragers													
Plecotus auritus/P. austriacus	DD/LC	LC/LC	1	0	0	0	1	0	0	0	0	0	0
Edge foragers													
Barbastella barbastellus	DD	NT	4	0	0	0	1	3	0	0	0	0	0
Myotis daubentonii	LC	LC	4	0	0	0	0	1	1	1	1	0	0
M. escalerai	-	-	6	1	0	0	1	0	3	0	1	1	0
M. myotis/M. blythii	VU/CR	LC/LC	15	1	0	0	6	0	2	3	1	3	0
Pipistrellus kuhlii	LC	LC	2	0	0	0	0	0	0	1	1	0	0
P. pipistrellus	LC	LC	113	3	5	29	6	9	2	15	15	7	30
P. pygmaeus	LC	LC	911	86	80	153	58	95	53	97	123	87	245
Open-space foragers													
Eptesicus serotinus/E. isabellinus	LC/ -	LC/ -	134	2	0	13	38	9	12	17	10	12	23
Nyctalus lasiopterus/N. noctula	DD/DD	NT/LC	12	0	0	2	2	1	1	1	2	2	1
N. leisleri	DD	LC	26	0	0	0	10	2	2	7	0	2	3
Tadarida teniotis	DD	LC	34	0	0	0	1	1	2	5	14	9	2

Because overall bat activity was biased due to the high number of passes recorded for some species (e.g. over 75% of all bat passes were attributed to *Pipistrellus spp.*), we reran the models without the *P. pygmaeus* passes and carried out multiple comparisons. Again, we found no significant differences in bat activity between habitat types. The model only containing habitat type best explained the variation in overall bat passes, with the model incorporating both habitat type and season as independent variables also providing a good fit (ΔAIC<2).

Table 3.2 Mean values for diversity, evenness and species richness for Spring, Summer and Autumn, on all of the eight habitat types studied. Habitat types abbreviations as summarized in Table 3.1.

	Habitat type							
Index/Season	*Boc*	*For*	*Mai*	*Mar*	*Ree*	*Ric*	*Rus*	*Urb*
D								
Spring	2.34	2.83	2.99	3.07	3.26	2.89	2.84	2.00
Summer	1.50	3.10	2.82	1.72	2.76	1.55	2.20	2.24
Autumn	1.93	2.13	1.08	1.66	2.07	2.77	1.90	1.40
E								
Spring	1.75	2.04	2.05	2.54	2.35	2.37	2.17	1.72
Summer	1.59	2.37	2.03	2.19	1.81	1.31	2.26	2.08
Autumn	2.00	2.11	NA[1]	2.34	1.89	2.30	1.57	1.70
S								
Spring	4.00	4.00	4.33	3.67	4.00	3.67	4.00	3.33
Summer	2.33	4.33	4.00	2.33	4.67	3.33	2.67	3.00
Autumn	2.67	3.00	1.33	2.00	3.00	3.33	3.33	2.33

[1] Since only one species was registered in Autumn on maize fields, by its definition, evenness is not applicable

Also, habitat type did not seem to influence the number of feeding buzzes recorded. Social calls, on the contrary, differed significantly between the urban and remaining habitats (p<0.01); though it should be noted that all the acoustic social behaviour registered belonged to species of the genus *Pipistrellus*, particularly to *P. pygmaeus* (Table 3.1). The summaries of the models presenting best fit are presented in Table 3.3.

The analysis of activity per guild revealed that edge foragers were significantly more active in urban areas, when compared to forest and marshlands (z=3.19, p=0.03 and z=3.50, p=0.01, respectively). However, once we repeated the analysis without *P. pygmaeus*, we found no significant differences in the activity of this guild between habitat types. Also, we found no significant differences between habitats in the activity of open-space foragers.

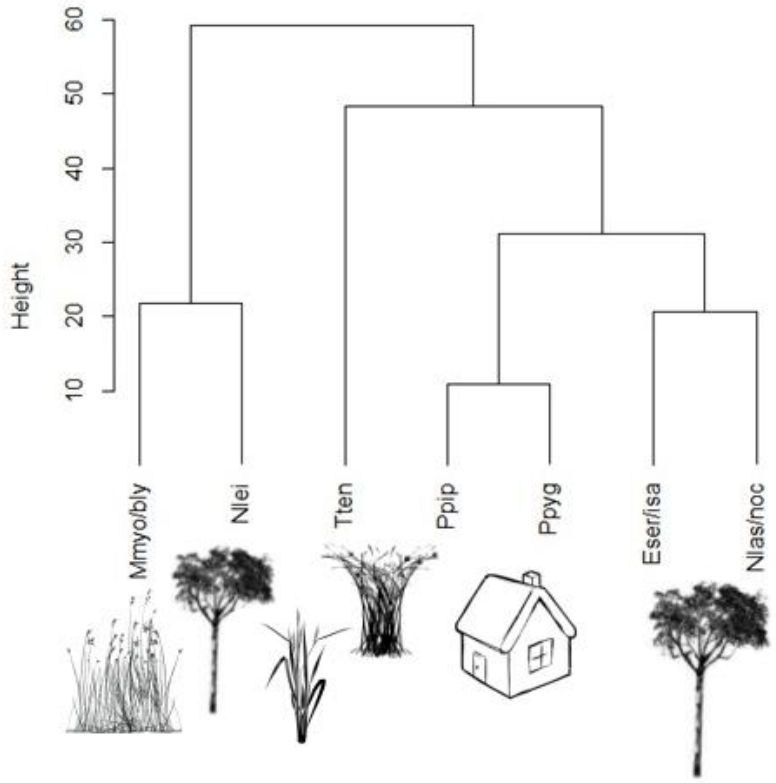

Figure 3.2 Dendrogram resulting from the cluster analysis of percentage of habitat use, and representation of the most used habitat types by each of the resulting clusters.

Habitat type significantly influenced the activity of *N. leisleri* and *P. pygmaeus*. The activity of *N. leisleri* was significantly higher in forest patches compared to rice fields or *Bocage* (z=3.57; p<0.01). Nearly significant differences were also found for *N. leisleri* between forest sites and maize fields (z=2.83; p=0.08), and between sites of sea rushes and marshlands (z=2.78; p=0.10). *P. pygmaeus* had higher levels of activity in urban environments. Significant differences between this habitat and five others were found for this species: marshlands (z=4.33; p<0.01), forest (z=4.03; p<0.01), sea rushes (z=3.43; p=0.01), reed beds (z=3.15; p=0.04) and maize fields (z=3.10; p=0.04).

The remaining five species considered in this approach revealed no significant differences in activity amongst habitat types. The summary of the GLMM performed for each species is presented in Table 3.3.

Seasonal patterns in bat assemblage structuring and activity

Species richness and diversity were significantly higher in Spring compared to Autumn (z=3.20, p<0.01 and z=3.73, p<0.01, respectively). Evenness was significantly higher in Summer compared to Autumn (z=3.61, p<0.01). As expected, bat activity was greatly reduced during the Winter so this season was excluded from the analysis.

Overall bat activity, feeding activity and social behaviour did not vary significantly between seasons. However, within seasons, significant differences were found in overall bat activity among the studied habitat types. During the Spring, higher activity levels were recorded in urban, *Bocage* and maize field habitats. Significant differences were found between urban sites and the remaining habitat types (all p <0.01), with the exception of *Bocage* and maize fields.

In Summer, rice fields and urban sites presented significantly more activity than the other habitats (all p<0.01), but these two habitat types were not significantly different from each other in terms of this parameter. The least used habitat type was marshlands, which revealed significantly less activity compared to forests (z=-3.32, p=0.02), reed beds (z=-3.72, p<0.01), urban (z=-4.52, p<0.01) and rice fields (z=-6.61, p<0.01).

During Autumn, the highest levels of bat activity were registered in urban and *Bocage* sites, as occurred during Spring, but also on reed beds. We found significant differences in bat activity between urban sites and the remaining habitat types (all p<0.01). Significant differences in bat activity were also found in *Bocage* and reed beds when compared to forest, marshlands, maize and rice fields (all p<0.01). Maize fields and marshlands presented the lowest bat activity levels, and also revealed less activity when compared to the sea rushes habitat (z=-3.53, p<0.01 and z=-4.66, p<0.01, respectively).

We found significant differences between seasons in the activity of the open-space foragers. This guild showed higher levels of activity in Spring than Autumn (z=3.93, p<0.01) and Summer (z=2.69, p=0.02). In contrast, the activity of edge foragers did not change significantly across seasons. Regarding the species-specific temporal patterns, our results only revealed statistically significant differences in the activity of *T. teniotis*,

with higher levels of activity registered in Spring compared to Summer (z=2.75, p=0.02) and Autumn (z=2.76, p=0.02). All models performed for seasonality are summarized in Table 3.3.

Table 3.3 Summary of the models performed, using as fixed variables habitat type, season, and a combination of both, and respective values of deviance, Akaike Information Criterion (AIC), and a measure of a model relative to the best model (ΔAIC).

Dataset	Model	Deviance	AIC	ΔAIC
Overall bat activity	Null	1225	1230	15
	Habitat	1212	1215	0
	Season	1223	1231	16
	Habitat+Season	1210	1216	1
Feeding activity	Null	408.7	418.7	0
	Habitat	405	439.5	20.8
	Season	408.7	428.5	9.8
	Habitat+Season	404.9	449.2	30.5
Social behaviour	Null	476.2	485.7	8.6
	Habitat	439.2	477.1	0
	Season	472.2	490.9	13.8
	Habitat+Season	434.8	482.3	5.2
Edge foragers	Null	320.2	326.2	15.8
	Habitat	304	310.4	0
	Season	320	329.1	18.7
	Habitat+Season	303.5	313.3	2.9
Open-space foragers	Null	151.9	161.1	7.5
	Habitat	140.3	169.9	16.3
	Season	136.8	153.6	0
	Habitat+Season	126.7	162.9	9.3
E. serotinus/ *E. isabellinus*	Null	107.7	117.5	0
	Habitat	95.21	129.7	12.2
	Season	106.7	124.7	7.2
	Habitat+Season	94.03	137.1	19.6
M. myotis/*M. blythii*	Null	80.79	68.4	48.06
	Habitat	88.03	33.14	12.8
	Season	81.46	55.6	35.26
	Habitat+Season	88.77	20.34	0

Dataset	Model	Deviance	AIC	ΔAIC
N. lasiopterus/	Null	143.4	130.1	61.45
N. noctula	Habitat	144.4	83.23	14.58
	Season	143.9	115.4	46.75
	Habitat+Season	144.9	68.65	0
N. leisleri	Null	89.52	77.46	38.55
	Habitat	108.2	51.04	12.13
	Season	91.61	65.32	26.41
	Habitat+Season	110.3	38.91	0
P. pipistrellus	Null	66.61	75.86	0
	Habitat	60.73	89.99	14.13
	Season	64.73	84.5	8.64
	Habitat+Season	58.62	98.64	22.78
P. pygmaeus	Null	296	302.4	16
	Habitat	274.1	286.4	0
	Season	295.2	305.4	19
	Habitat+Season	273.1	289.3	2.9
T. teniotis	Null	49.57	60.15	0
	Habitat	42.89	83.24	23.09
	Season	39.71	60.53	0.38
	Habitat+Season	32	83.66	23.51

3.4. DISCUSSION

Bat assembly structuring across habitats and seasons

We found no significant differences in bat assemblage structure and composition among the different studied habitat types of the BVL landscape. This is in accordance with other studies showing that bats explore different patches within a landscape, and that fragmented, mosaic-shaped landscapes can still harbour several bat species (Law and Dickman, 1998; Bernard and Fenton, 2002, 2007). On the other hand, it might also suggest the presence of one assemblage making use of several distinct habitat patches. This may be the case if chosen sampling sites are close to each other, since some of the registered species have small home-ranges (e.g. *P. pipistrellus* and *P. pygmaeus* – Nicholls and Racey, 2006; *Myotis myotis* – Drescher, 2004), but not if sampling sites are several kilometres apart. Frequent movements between roosting and foraging sites located far apart are only possible for species known to fly long

distances and to possess large home-ranges (e.g. *N. leisleri* – Shiel et al., 1999; *T. teniotis* – Marques et al., 2004). In any case, land cover does not seem to strongly influence the occurrence of a species in a certain site within the BVL landscape, possibly due to the generalist character of the studied species (four of the seven most recorded species were registered in all sampled habitat types). We found significant variation in bat diversity, richness and evenness throughout the study period, which may be due to the temporal dynamics of resource distribution, such as prey and/or appropriate roost availability.

We found similar values of species richness and diversity in forest sites when compared with the other studied habitats. However, evergreen woodlands, including *Eucalyptus* stands (which comprised the majority of our forest sites), are often associated with lower animal diversity and species richness, both in bats (Russo and Jones, 2003; Matos, 2011) and other *taxa* (Marsden et al., 2001; Zahn et al., 2009). The importance of broadleaved woodlands for several European bat species as foraging (Walsh and Harris, 1996; Russ and Montgomery, 2002; Rainho, 2007; Sattler et al., 2007) and roosting habitats (Russo et al., 2004; Dietz et al., 2009; Boughey et al., 2011) is well known. However, evergreen woodlands, especially well-developed stands, may increase in importance when broadleaved woodlands are absent. Also, we expected species richness and diversity to be lower in urban sites, since only the most ubiquitous species often forage in these areas (Rydell, 1992). Although six of the twelve recorded species were not observed in urban sites during this study, the values of diversity and species richness did not differ significantly from those of other habitat types; although this may be due to a lack of statistical power.

Spatial and seasonal patterns of activity

Overall, we found few differences in the activity patterns of the different bat species across habitats. We found a positive influence of urban sites on the activity of *P. pygmaeus*, which is not unusual for this species (Rainho, 2007; Pocora and Pocora, 2011). However, these bats are also usually found foraging in riparian sites (Vaughan et al., 1997; Russo and Jones, 2003; Davidson-Watts et al., 2006; Lundy and Montgomery, 2010), deciduous woodland (Glendell and Vaughan, 2002; Pocora and Pocora, 2011), woodland edges and other linear features such as hedgerows and tree lines (Glendell and Vaughan, 2002; Brandt et al., 2007). Other species of the genus *Pipistrellus* such as *P. kuhlii* and *P. pipistrellus* are known to forage in a wide range of habitat types and often feed around streetlamps (Blake et al., 1994; Carmel and Safriel,

1998; Russo and Jones, 2003) but *P. pygmaeus*, by comparison, seems to be more of a specialised and selective species (Davidson-Watts et al., 2006). The proximity of human settlements to wetlands and riparian habitats in the BVL landscape may provide *P. pygmaeus* with additional suitable foraging habitats, particularly surrounding streetlights in human settlements where high densities of prey may occur (Gaisler et al., 1998; Rydell, 1992; Avila-Flores and Fenton, 2005). Our cluster analysis also revealed a positive tendency for more activity of both *P. pygmaeus* and *P. pipistrellus* in *Bocage*. The dense network of linear structures such as live fences found in this habitat type may provide optimal foraging sites and commuting routes for these species, as well as protection against predators and adverse weather conditions (Verboom and Huitema, 1997). These hedgerows, together with the numerous freshwater sources available in this habitat, also provide favourable conditions for many insect species (Harvey et al., 2005; Verboom and Huitema, 1997), thereby increasing their abundance and, presumably, their availability to bats. Indeed, the short wingspan and manoeuvrable flight of *Pipistrellus*, as well as the FM and QCF components of their search calls, enables them to forage close to vegetation in background-cluttered spaces (Schnitzler and Kalko, 2001), ultimately giving them an advantage in exploiting such habitat.

We also found a positive relation between forests and the activity of *N. leisleri*. Although woodland habitats or their edge structures are regarded as some of the preferred roosting and foraging habitats of this species (Dietz et al., 2009), some studies have demonstrated that *N. leisleri* often exhibits no habitat preferences, reflecting a somewhat generalist choice of foraging habitats (Russ and Montgomery, 2002; Lundy and Montgomery, 2010). Also, Shiel and Fairley (1998) and Pocora and Pocora (2011) found higher levels of activity of this species in human settlements, particularly along roads and streetlamps. In this study, *N. leisleri* occurred in six of the eight studied habitats; though we cannot be sure whether the bats were foraging or just commuting. Through hierarchical clustering, some similarities were found between *N. leisleri* and *M. myotis*/*M. blythii* regarding percentage of habitat use (see Fig 2). Because *M. myotis* forages on the ground (Audet, 1990) and *N. leisleri* often forages over the canopy (Dietz et al., 2009), they are likely to explore different space and prey resources in similar habitat types.

We found a positive influence of urban sites on overall bat activity, feeding activity and social behaviour, as well as in the activity of the edge-foragers guild. However, this bias towards urban environments is undoubtedly linked to the activity of *P. pygmaeus*, already described above. Despite that no differences were found between habitat types

for the activity of the open-space foragers guild, we found some similarities in the percentage of habitat use between *E. serotinus*/*E. isabellinus* and *N. lasiopterus*/*N. noctula* through the cluster analysis. Furthermore, this analysis confirmed the preference of *T. teniotis* for open-space, uncluttered habitats since this species almost exclusively used this type of setting and, particularly, rice fields, sea rushes and reed beds.

Bat activity in the different habitat types varied throughout the study period. Since some insect prey is known to be more abundant during short periodic bursts of time (in a process called swarming) that can occur at different times of the year in distinct habitat types (de Jong and Ahlén, 1991), our results may reflect the response of bats to these shifts in prey availability (Robinson and Stebbings, 1997), as well as to the characteristic temporal heterogeneity of human-altered landscapes (DeCleck et al., 2010).

The higher activity of the open-space foragers guild and of *T. teniotis* in Spring may be explained by post-hibernation restoration of fat reserves (Ciechanowski et al., 2010). However, since pregnancy and lactation occur during summer, bat activity was expected to be higher in this season due to the increased energy demands of these life-cycle stages (Kunz, 1973; Encarnação and Dietz, 2006). However, the lower activity during the summer observed in this study might be explained by the fact that bat detectability was lower during this season due to significant noise disturbance produced by katydids. This is especially relevant for species with low-frequency calls, such as *T. teniotis* and those of the genus *Nyctalus*, since katydid song is usually emitted between 600Hz and 20kHz (del Castillo and Gwynne, 2007), corresponding partially or completely to the frequency intervals of their echolocation calls. The lower activity registered during the autumn might reflect bat dispersal to distant winter hibernacula.

Heterogeneous landscape matrices as mosaics of opportunities

Since few differences were found amongst the habitat types studied, two main scenarios can be considered: 1) landscape matrices can be regarded as mosaics of opportunities, enabling bats to exploit vital resources in distinct patches; 2) opportunities are scarce in fragmented landscapes, forcing bats to exploit less optimal habitats and resources.

For the first scenario, we attribute the lack of differences to the generalist character of some of the recorded species (e.g. *E. serotinus* – Rainho, 2007; *N. leisleri* – Lundy and

Montgomery, 2010; *P. pipistrellus* – Russo and Jones, 2003), and to a response by bats to temporal and spatial variation in resource availability. The response of bats to changes in resource availability, particularly to prey availability, has been described for some species such as *E. serotinus* (Robinson and Stebbings, 1997) and *Pipistrellus* species (Kusch and Idelberger, 2005). In fact, changes in food supply are considered to be one of the key factors behind seasonal changes in bat activity (Bartonicka and Zukal, 2003; Meyer et al., 2004; Ramos Pereira et al., 2010). Therefore, the observed fluctuation in use of foraging sites during the year can be interpreted as an exploitation of insect concentrations, rather than a consistent use of particular habitats (Swift et al., 1985; Furlonger et al., 1987; Kusch and Idelberger, 2005). Bats usually require a mixed landscape in which adequate foraging, roosting and drinking sites can be found (Lookingbill et al., 2010). These vital habitats and resources are frequently widely scattered within the landscape. However, many species of bats are highly vagile and move readily within the landscape matrix to take advantage of the different available patches (Medina et al., 2007; Rainho and Palmeirim, 2011). Thus, combining the temporal and spatial variation of resource availability, the mobility of bats, their need for different habitats within a landscape, and the opportunistic character of most species, we assume that bats interpret the BVL landscape matrix as a whole, rather than selecting or exploiting the different habitat types individually. In this way, the heterogeneous landscape that characterizes the BVL region provides a mosaic of opportunities for bats, which freely exploit the resources across different land cover settings and according to their temporal variation. This is consistent with other studies that revealed that fragmented landscapes can still harbour high bat species richness and abundance, and that bats exploit the different settings present in the landscape (Bernard and Fenton, 2002; Estrada and Coates-Estrada, 2002; Gorresen and Willig, 2004; Bernard and Fenton, 2007).

The second scenario presents a more pessimistic view of the interaction between bats and the heterogeneous landscape. There are several known negative effects of fragmentation on animal species (e.g. Saunders et al., 1991). The intensification of agriculture (Wickramasinghe et al., 2003), pesticide use (Racey and Entwistle, 2003) and transformation of natural habitats into monocultures (Lacki et al., 2007) are also know to negatively influence bat diversity and populations. Since the BVL landscape is composed of a mosaic of natural and human-altered habitats, with significant coverage by agricultural fields (intensive and extensive) and forest monocultures, those negative effects are probably present. Since resource availability directly influences the development and maintenance of individuals and populations, anthropogenic changes that alter their abundance and distribution in space and time can have considerable

negative impacts on animal communities (Bradbury et al., 2001). Furthermore, human alterations of natural ecosystems may reduce the availability of optimal habitats, forcing some organisms to explore sub-optimal patches to which they might not be well-adapted (Lambrechts et al., 2004). If that is the case in our study area, the scarcity of resources may be forcing bats to exploit the several habitat types that shape the landscape, regardless of their particular setting. This would explain the similar assemblages found over the different habitats, as well as the lack of differences found in the activity of guilds and species amongst them.

Despite the fact that both scenarios could explain our findings, we believe that the particular case of the BVL landscape is closer to the first one, at least for some of the recorded bat species. Although some of the above-mentioned negative effects of human activities are probably affecting bat communities, it seems plausible that several of the bat species recorded, particularly the more opportunistic ones, still have an adequate mosaic of habitats where foraging and roosting sites can be found. Since large wetland and riparian areas, closely located to other habitats, characterize the BVL landscape, we believe that bats exploit the landscape as a whole, taking advantage of the resources available in different areas at different times of the year. Nevertheless, this may not be true for some of the species found in this study. The loss of important habitats, such as broadleaved woodland that has been transformed into agricultural land and evergreen forest monocultures, may negatively influence the strict forest-dwelling species, namely *B. barbastellus* and *Plecotus* spp., which were rarely recorded during this study.

Chapter 4

BAT RICHNESS AND ACTIVITY IN HETEROGENEOUS LANDSCAPES: GUILD-SPECIFIC AND SCALE-DEPENDENT?

4. BAT RICHNESS AND ACTIVITY IN HETEROGENEOUS LANDSCAPES: GUILD-SPECIFIC AND SCALE-DEPENDENT?

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4.1. ABSTRACT

The conversion of natural environments into agricultural land has profound effects on the composition of the landscape, often resulting in a mosaic of crop fields, pastures and remnant patches of natural vegetation. Although an increase in structural complexity of a habitat mosaic may improve the availability of ecological niches for animals, potentially increasing species diversity, the responses of organisms to these changes will be species-specific and scale-dependent. Bats are highly vagile, and their daily and seasonal resource needs often require the use of distinct habitats. Furthermore, the way they select a habitat is an aggregative response to both landscape and local features. We sampled bats acoustically, while simultaneously sampling insects with light traps, across 24 sampling sites within a heterogeneous landscape in Portugal, constituted by a mosaic of natural, semi-natural and human-altered terrestrial and freshwater and brackish habitats. We then assessed the relationships between total bat activity, activity of distinct guilds, and species richness, with landscape and local features, across four distinct focal scales. Our results revealed both scale- and guild-dependent responses of bats to landscape and local features. At broader scales we found positive associations between open-space

foraging bats and habitat heterogeneity and, as expected, between edge-space foraging bats and greater edge lengths. At smaller scales, forest cover and water availability (for open-space foragers) and *Bocage* cover (for edge foragers) were the most efficient predictors. Locally, bat activity was strongly associated with weather conditions and insect abundance. Globally, our results suggest that bats are sensitive to local resource availability and distribution, while simultaneously reacting to broader landscape features. Also, our results suggest that forest and *Bocage* habitats are potential keystone structures for bats within this heterogeneous landscape.

4.2. INTRODUCTION

Land use change happens through both natural and anthropogenic processes. However, human actions are responsible for unprecedented and profound modifications on ecological systems worldwide (Lambin et al., 2001). In Europe there are hardly any landscapes that are not under any type of human influence (Meeus, 1995), and farmland nowadays represents the majority of the land cover in the European territory (Robinson and Sutherland, 2002, Billeter et al., 2008).

One of the most frequent changes is the conversion of natural habitats into agricultural land. The result is often the fragmentation of natural habitats (Haila, 2000) by the immersion of those remnant natural patches in a human-managed, agricultural matrix (Uematsu et al., 2010; Fuentes-Montemayor et al., 2013). Indeed, in Europe, agricultural landscapes are usually composed by a mosaic of crop fields, pastures and natural remnant patches, creating a landscape of high spatial (Duchamp and Swihart, 2008) and temporal heterogeneity dictated by human activities and land management (Di Giulio et al. 2001; DeClerck et al. 2010; Gilroy et al. 2010). The increase in agriculture intensity and land abandonment are some of the main causes for biodiversity loss worldwide (Meeus, 1995; Lambin et al., 2001; Robinson and Sutherland, 2002; Uematsu et al., 2010), but low-intensive land-use systems may actually be positive for biodiversity conservation (Tscharntke et al., 2005).

The “habitat heterogeneity hypothesis” assumes that an increase in structural complexity of a habitat mosaic leads to the availability of more ecological niches, and promotes several distinct opportunities for resource exploitation, resulting in greater species diversity (Bazzaz, 1975; Tews et al., 2004). Still, spatial heterogeneity affects the dispersal patterns of organisms, as well as their foraging behaviour (Johnson et al., 1992), since resource availability may vary in different regions of the landscape, altering their suitability to the organism (Milne et al., 1989). However, the response of

an organism to spatial heterogeneity depends strongly on its taxonomic group, its dispersion abilities, and its perception of the surrounding habitat (Kotliar and Wiens, 1990; Malanson and Cramer, 1999; Tews et al., 2004). This response is also scale-dependent, since a heterogeneous landscape likely to be easily explored by an organism might be impossible to exploit by another (Milne et al., 1989) due to eco-morphological restraints.

Bats are highly vagile, and many species depend on multiple habitats to fulfil their daily and seasonal needs, especially to deal with different requirements along the various stages of their life-cycle (Law and Dickman, 1998; Lookingbill et al., 2010). The process of habitat selection, i.e. their presence and use of a certain site within a landscape, results from a set of decisions at both the landscape and local scales (Ford et al., 2006). On a wider scale, bats are thought to respond to landscape configuration (e.g. patchiness, habitat diversity, land cover proportions), roost availability, proximity to adequate foraging sites and water sources, climatic conditions and anthropogenic disturbance (Furlonger et al., 1987; Gehrt and Chelsvig, 2003; Evelyn et al., 2004; Ford et al., 2006; Johnson et al., 2008, Rainho et al., 2010). Locally, vegetation structure, eco-morphological traits and prey availability seem to be some of the most influential factors (Aldridge and Rautenbach, 1987; Ford et al., 2005, 2006; Johnson et al., 2008). Furthermore, bats also exhibit strong seasonal dynamics in activity and habitat use; this usually reflects the weather conditions, (e.g. winter survival or hibernation), the directly or indirectly related changes in prey availability, and the stage of the life-cycle (Bartonicka and Zukal, 2003; Meyer et al., 2004; Ciechanowski et al., 2010; Wang et al., 2010),

Several studies have looked into the interaction between bats and the features of the landscape they inhabit, but they have mainly focused forested areas (e.g. Yates and Muzika, 2006; Perry et al., 2008), particularly in the tropics (e.g. Gorresen and Willig, 2004; Gorresen et al., 2005; Pinto and Keitt, 2008; Klingbeil and Willig, 2009). Though some studies have recently looked into the responses of bats to landscape features in predominantly agricultural landscapes in temperate regions (e.g. Duchamp and Swihart, 2008; Popa-Lisseanu et al., 2009; Ethier and Fahrig, 2011; Fuentes-Montemayor et al., 2011, 2013; Rainho and Palmeirim, 2013) there are still important gaps concerning the knowledge of the patterns of bat occurrence in those landscapes and, most importantly, of the processes behind those patterns. Fuentes-Montemayor et al. (2011) and Duchamp and Swihart (2008) found a positive influence of the amount of forest cover on bat abundance, reinforcing the importance of woodland patches in landscapes where this habitat type is scarce. However, in both studies the response differed between species, according to their mobility and roosting preferences.

Fuentes-Montemayor et al. (2013) and Rainho and Palmeirim (2013) also found species-specific responses to landscape features on multispecies colonies, mainly driven by their degree of habitat specialization. Ethier and Fahrig (2011) found a positive influence of fragmentation on bat abundance, stating that landscape complementation is the main mechanism supporting that relationship. On the other hand, the results obtained by Popa-Lisseanu et al. (2009) showed a negative influence of habitat fragmentation on the populations of *Nyctalus lasiopterus* due to the increase of the distances between adequate roosting and foraging habitats (i.e. low landscape complementation, Dunning et al., 1992).

In this study, we aim to investigate the relation between bat activity and species richness and the heterogeneous landscape of Baixo Vouga Lagunar, Central-West Portugal, through a multi-scale approach. Specifically, we aim to i) identify the landscape and local features that better explain bat activity and richness within the study area; ii) investigate if the response given by bat activity and richness to landscape characteristics varies across a gradient of focal scales; and iii) investigate how different bat guilds respond to landscape and local features.

With this we expect to be able to understand factors affecting bat activity and richness within the Baixo Vouga Lagunar matrix, so that future research, conservation and land management plans may be supported on solid bases. Furthermore, we expect that the knowledge acquired with this study may also help in the interpretation of the relationship between bats and human-altered, heterogeneous landscapes elsewhere.

4.3. MATERIALS AND METHODS

Study area

The study area has an area of approximately 50,000 ha, and is located in the Aveiro district, on the Central-North Portuguese coast (Figure 4.1). It harbours the municipalities of Albergaria-a-Velha, Aveiro, Estarreja, Ílhavo, Murtosa, Oliveira de Azeméis and Ovar (40º39-52'N, 8º27-45'W), encompassing the Baixo Vouga Lagunar (BVL), as well as its surroundings. Hereafter we refer to our study area as BVL, although it encompasses a significant extension of its surroundings. The landscape is characterized by a heterogeneous landscape, with a mosaic of natural, semi-natural and human-altered habitats. The natural habitats include aquatic and terrestrial

environments, in particular the Ria de Aveiro, an estuarine coastal lagoon. Over 34% of the area is occupied by agricultural land, both traditional and intensive.

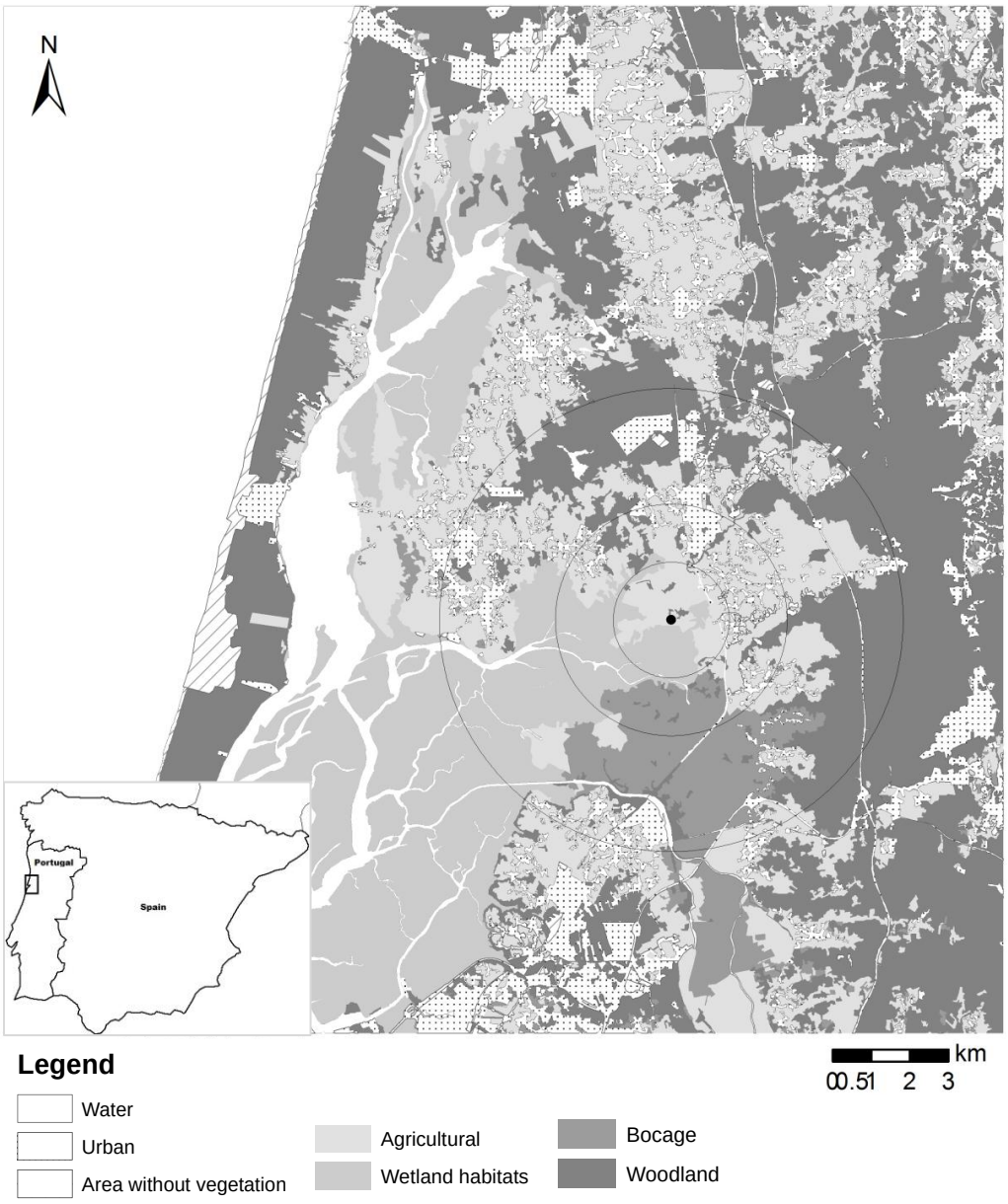

Figure 4.1 Approximate location of the study area in the Iberian Peninsula, main land use characterization, and example of a sampling site and respective buffers of 1.5 km, 3 km and 6 km, used for landscape analysis.

The traditional form of agriculture is represented by the *Bocage*, which is a unique man-made habitat, characterized by small areas of crops and pastures, intersected by small freshwater courses and live fences of autochthonous trees (e.g. *Alnus glutinosa, Salix atrocinerea, Quercus robur*), shrub and herb hedgerows (e.g. *Hedera* spp., *Rubus*

spp.). In Portugal, this type of agricultural practice is limited to the BVL region, and otherwise in Europe only to southern France and northern England (Brito et al., 2010). The remaining agricultural lands are dedicated, to a small extent, to rice (*Oryza* sp.) production, and to a greater extent and more intensively, to maize (*Zea mays*) cultures. Woodlands are fragmented, and mostly composed by production, non-deciduous tree species, mainly *Eucalyptus globulus*, but also *Pinus pinaster*). Several villages, as well as numerous industries can be found both within and in the outskirts of BVL.

This region is a transition zone between the Atlantic and the Mediterranean climates, with a strong influence from the Atlantic Ocean (Costa et al., 1998; Bonmatí et al., 2006). During the study period (October 2011 - September 2012), mean air temperature was 14.5 ºC (oscillating between 8.5 ºC in February and 19.8 ºC in September), and mean annual humidity of 76.5% (data from CUF weather station). Accumulated precipitation varied between 5.6 mm in July and 194 mm in November, with an annual value of 627.6 mm (data from CESAMET).

Bat sampling, identification and definition of eco-morphological guilds

We sampled bats acoustically through 15-minute walking surveys, of approximately 500 m, performed at a regular pace. Sampling was carried out on a total of 24 sites, divided in three replicates of eight habitat types characteristic of the BVL landscape: *Bocage*, forest, maize fields, marshlands, reed beds, rice fields, sea rushes and urban. We sampled each site twice a month, so that the variation between nights and sites could be taken into account (Broders, 2003; Wickramasinghe et al., 2003; Ford et al., 2005). No sampling was performed on nights with unfavourable weather conditions such as rain or strong winds, since these are known to negatively influence bat activity (Ford et al., 2005, 2006) and detectability (Dixon, 2012). During April and July, there were adverse weather conditions, thus we were only able to sample once on each of these months.

We performed the walking surveys within the first 2.5h-3h after dusk, when bat activity levels are highest (Rydell et al., 1996; Hayes, 1997), using a Pettersson D240x ultra-sound detector (Pettersson Elektronik AB™, Uppsala, Sweden) in heterodyne mode. To maximize the chance of detecting different bat species, we travelled at a constant and fast pace through the full range of frequencies (Russ and Montgomery, 2002). A digital recorder (Edirol R-09, Roland Corp., Shizuoka, Japan) was used to storage the 1.7 seconds sample calls. For every transect, we registered air temperature, relative humidity, atmospheric pressure and wind velocity using a Kestrel 4000 hand-held weather station (Kestrel Meters™, Birmingham, Michigan).

We analysed bat calls with Audacity 1.3.13 software (http://audacity.sourceforge.net), and registered several parameters: call duration, inter-pulse interval, start and end frequencies and peak frequency (frequency containing most energy). Whenever possible, we identified calls to the species level, using a reference collection of bat calls and dichotomous keys for Portuguese (Rainho et al., 2011) and Iberian (Lisón, 2011) bats. We then divided bat species into three guilds, based on eco-morphological traits (Fenton, 1990; Schnitzler and Kalko, 2001):

i) Open-space foragers – Species that emit long, narrowband and low-frequency calls, and are characterized by a fast and energetically inexpensive flight, with high wing loading and aspect ratio. Species included in this guild were *Nyctalus* spp., *Eptesicus* spp. and *Tadarida teniotis*;

ii) Edge-foragers – Species that echolocate through short pulses often composed of both broad and narrowband components, that present a slow and energetically inexpensive flight type, and average wing loading and aspect ratio. Species included in this guild were *Barbastella barbastellus*, *Myotis* spp. and *Pipistrellus* spp.;

iii) Closed-habitat foragers (CHF) – Species with low-intensity, broadband echolocation calls, characterized by low wing loadings and aspect ratio, and that present a very manoeuvrable, but energetically expensive flight. Species classified as closed-habitat foragers were those of the genus *Plecotus*.

Insect sampling

Insects were sampled using light traps, on the same sites where bat surveys were performed. The place where traps were set up was selected so that a compromise between the representativeness of the sampled habitat type and trap protection against theft and destruction was achieved. Placement sites where kept constant throughout the study period. Traps contained a tubular fluorescent actinic light (8W), frequently used to attract and capture insects (e.g. Sutton and Hudson, 1980; Birkinshaw and Thomas, 1999; Davis et al., 2011). We set the traps in the field before nightfall, prior to the walking surveys, within the path of the walking transects, and those were on for approximately two hours. Insect and bat sampling occurred simultaneously, but due to light traps' theft, component malfunction or adverse weather conditions, the two monthly samples were not always possible. Captured insects were collected and stored in 70% ethanol for posterior identification in the laboratory. All insect sampling was carried out under the licenses number 385 / 2011/ CAPT and 99 / 2012 / CAPT (ICNF, Instituto da Conservação da Natureza e das Florestas). We identified the arthropods to

the order level, using appropriate literature and dichotomous keys (e.g. Barrientos, 1988; Chinery, 2007; Capinera, 2008), and total abundance was registered for each order and site.

Landscape predictors

We used ArcGIS 10.0 to create buffers of 1.5, 3 and 6 km radii around the mid-point of each transect. The different scales used intend to cover the known home ranges of the detected species, with low (e.g. *P. pygmaeus*, Nicholls and Racey, 2006), intermediate (e.g. *M. myotis*, Drescher, 2004), and high (e.g. *N. leisleri*, Shiel and Farley, 1999; *T. teniotis*, Marques et al., 2004) mobility. We used data from COS2007 (IGP, 2010) to classify the landscape into land cover types, and updated it so that it could include recent modifications, verified by us during dedicated field incursions and satellite imagery. For every buffer we calculated the percentage of each land cover class, and categorize them into six types: i) rice fields; ii) *Bocage*; iii) forest; iv) maize fields; v) wetland habitats (joint percentage of reed beds, sea rushes and marshlands); and vi) human (joint percentage of urban and industrial areas). Using ArcGIS, we also withdrew values of total edge (i.e. total length of the boundaries between adjacent patches of different land cover types) and watercourse lengths. We used Fragstats 4.1 (McGarigal et al., 2012) and selected and calculated four landscape metrics: i) patch density (PD: number of patches per 100 ha); ii) Shannon diversity index (SHDI: landscape heterogeneity index); iii) area-weighted mean patch shape index (SHAPE_AM: measure of patch shape complexity, taking into account patch areas); and iv) contagion (CONTAG: index of landscape connectivity – considers both the dispersion and interspersion of patch types). The abovementioned variables (Table 4.1) were chosen so that both landscape composition (e.g. land cover type proportions, watercourse length) and physiognomy (e.g. patch density, landscape connectivity) could be assessed (Dunning et al., 1992).

Local predictors

We used as local independent variables a set of weather, food availability, and habitat related predictors (Table 4.1). Weather predictors included air temperature and relative humidity, atmospheric pressure and wind velocity. Food availability predictors included the total number of insects captured, and the total number of individuals belonging to the orders Diptera, Lepidoptera, Coleoptera, Himenoptera and Hemiptera. We chose these orders because they were the most common in the captures and due to their

documented importance to the diet of insectivorous bats, particularly concerning the species recorded in this study (e.g. Swift et al., 1985; Waters et al., 1995; Vaughan, 1997; Ramos Pereira et al., 2002; Kervyn and Libois, 2008; Dietz et al., 2009; Fuentes-Montemayor et al., 2013). Habitat type and the normalized difference vegetation index (NDVI) of each site were also considered as independent variables at the local scale.

Table 4.1 Classes of predictors, and predictors used to explain bat activity and species richness across three landscape scales (6 km, 3 km and 1.5 km) and at the local scale.

Predictor Class	Predictor	Landscape	Local
Food availability	Coleoptera		✓
	Diptera		✓
	Hemiptera		✓
	Himenoptera		✓
	Lepidoptera		✓
	Total Insects		✓
Landscape composition	Bocage (%)	✓	
	Forest (%)	✓	
	Human (%)	✓	
	Maize field (%)	✓	
	Rice field (%)	✓	
	Wetland habitats (%)	✓	
	SHDI	✓	
	Watercourse length	✓	
Landscape physiognomy	PD	✓	
	SHAPE_AM	✓	
	CONTAG	✓	
	Total edge	✓	
Habitat	Habitat type		✓
	NDVI		✓
Weather	Air temperature		✓
	Atmospheric pressure		✓
	Relative humidity		✓
	Wind velocity		✓

Statistical analysis

All statistical analysis were performed with software R, version 2.15.1 (R Core Team 2013), using the hier.part and lme4 packages. We used a hierarchical partitioning analysis (HPA, Chevan and Sutherland, 1991; McNally, 1996) to evaluate the

independent contribution of the 12 variables at the landscape and 12 variables at the local level to explain the variation of total bat activity, guild activity, and species richness. According to Olea et al. (2010), the HPA performed in the hier.part package for more than nine independent variables produces a considerable inconsistency, as the entering order of the variables affects their ranking. To avoid this bias (the probability of a variable changing its position), we performed the analysis with 100 repetitions, with different entering orders of the explanatory variables, as suggested by Olea et al. (2010). The models were fit to data by the least-squares method (i.e. goodness-of-fit measures calculated by R-squared). We then ranked the variables and selected the ones that presented the highest independent contribution towards the variation of each of the four response variables. For each response variable, a set of nine independent variables was chosen, since it was verified that, for this number and less, the ranking does not change with different entering orders (Olea et al., 2010). Then a randomization test (function “rand.hp”) was done with 100 randomizations, to assess the significance of each variable in explaining the variation of the four response variables. We then created a subset composed by the potential predictors that returned significant after this approach, for each response variable, and performed generalized linear models (GLM) for the landscape datasets (since the number of levels for the random effects – replicate - was equal to the number of observations), and generalized linear mixed models (GLMM) for the local dataset, to identify which of variables best predicted bat activity (total bat and guild activity) and species richness at each scale. Model selection was performed using Akaike’s Information Criterion (AIC).

Based on the results obtained both in HPA and model selection, we classified the relationships between response and explanatory variables similarly to Avila-Cabadilla et al. (2012). Three types of relationship are defined: i) robust: when a significant influence (significance level set at $p \leq 0.05$) was verified between the dependent and independent variables in the HPA, and the explanatory variable was selected as one of the best predictors in the models; ii) those denoting a tendency: when an explanatory variable explains a great amount of the variation of the response variable, but no significant relationship was found between them in the HPA, and it was selected as part of the best-fitted models; and iii) no relationship: when no significant or near significant relationship was found between response and explanatory variables in the HPA, and the explanatory variable was not selected in the best models.

4.4. RESULTS

Bat diversity

Through the total 1544 bat calls recorded during this study, we identified 12 species (or two-species complexes): *Barbastella barbastellus*, *Eptesicus serotinus*/*E. isabellinus*, *Myotis daubentonii*, *M. escalerai*, *M. myotis*/*M. blythii*, *Nyctalus lasiopterus*/*N. noctula*, *N. leisleri*, *Pipistrellus kuhlii*, *P. pipistrellus*, *P. pygmaeus*, *Plecotus auritus*/*P. austriacus* and *Tadarida teniotis* (Table 4.2). We were able to classify 1468 (95.1%) calls as belonging to species of the three guilds abovementioned. 245 calls (15.9%) were attributed to the open-space foragers, and 1222 (79.1%) to the edge foraging guild (Table 4.2). Since only one call was recorded for the closed-habitat foragers (*P. auritus*/*P. austriacus*), we excluded this guild from further analyses.

Insect abundance

A total of 40432 insects were captured, belonging to the orders Diptera, Himenoptera, Lepidoptera, Coleoptera, Dictyoptera, Hemiptera, Orthoptera, Embioptera, Neuroptera, Trichoptera, Psocoptera, Odonata and Dermaptera. The most frequent orders were Hemiptera (24895 individuals; 61.6%), Coleoptera (7188; 17.8%), Diptera (5361; 13.3%), Lepidoptera (2200; 5.4%) and Himenoptera (675; 1.7%). These five orders were selected as explanatory variables for the 12-variable dataset used in the HPA.

Relation between bat activity and landscape and local variables

Based on HPA results and model selection (Table 4.3 and Table 4.4, respectively), we found that total bat activity tended to be associated with different landscape predictors, at the different scales approached. At the 6 km focal scale, we found that bat activity tended to be negatively related to the percentage of forest cover, but positively associated with increasing areas of maize fields. At the 3 km scale, bat activity tended to be higher when larger extensions of *Bocage* were present. On the other hand, bat activity tends to be negatively associated with patch density and percentage of rice fields at this scale. Confining the scale to the 1.5 km level, a similar positive tendency was found between bat activity and the percentage of *Bocage* cover. Additionally, at the 1.5 km focal scale, bat activity tended to be positively linked with the percentage of rice field cover.

At the local scale, we found a robust positive association between bat activity and air temperature and Diptera abundance. Furthermore, bat activity tended to vary with habitat type (marginally non-significant higher activity on urban sites; p=0.08), and tended to be negatively related with atmospheric pressure.

Table 4. 2 List of species recorded, and respective classification in guilds and conservation status in Portugal (Cabral et al., 2005), and worldwide (IUCN, 2013), and total number of bat passes recorded in each habitat type. Habitat types abbreviations as: *Bocage* (Boc), forest (For), maize field (Mai), marshland (Mar), reed bed (Ree), rice field (Ric), sea rush (Rus) and urban (Urb).

Species	Status		Bat passes per habitat type							
	PT	IUCN	Boc	For	Mai	Mar	Ree	Ric	Rus	Urb
Closed-habitat foragers										
Plecotus auritus/P. austriacus	DD/LC	LC/LC	0	1	0	0	0	0	0	0
Edge foragers										
Barbastella barbastellus	DD	NT	0	1	3	0	0	0	0	0
Myotis spp.			1	1	7	1	3	0	0	0
M. daubentonii	LC	LC	0	0	1	1	1	1	0	0
M. escalerai	-	-	0	1	0	3	0	1	1	0
M. myotis/M. blythii	VU/CR	LC/LC	0	6	0	2	3	1	3	0
Pipistrellus spp.			19	6	9	2	15	15	7	30
P. kuhlii	LC	LC	0	0	0	0	1	1	0	0
P. pipistrellus	LC	LC	29	6	9	2	15	15	7	30
P. pygmaeus	LC	LC	153	58	95	53	97	123	87	245
Open-space foragers										
Eptesicus spp./*Nyctalus* spp.			2	3	2	0	0	2	3	1
Eptesicus serotinus/E. isabellinus	LC/ -	LC/ -	13	38	9	12	17	10	12	23
Nyctalus spp.			5	4	3	0	9	1	2	0
N. lasiopterus/N. noctula	DD/DD	NT/LC	2	2	1	1	1	2	2	1
N. leisleri	DD	LC	0	10	2	2	7	0	2	3
Tadarida teniotis	DD	LC	0	1	1	2	5	14	9	2

Table 4.3 Summary of the main results obtained on the HPA, for the four focal scales approached. *z*-scores are presented for the best predictors of the four response variables at each scale. Significant effects ($p \leq 0.05$) are signalled by an asterisk.

Response variable	Landscape						Local	
	6 km		3 km		1.5 km			
	Predictor	***z*-score**	**Predictor**	***z*-score**	**Predictor**	***z*-score**	**Predictor**	***z*-score**
Total bat activity	Forest	- 0.55	Bocage	0.63	Rice fields	1.14	Air temperature	30.59 *
	Maize fields	- 0.53	Patch density	- 0.52	Bocage	0.67	Diptera	3.01 *
	Patch density	- 0.63	Rice fields	0.44	Forest	- 0.65	Atmospheric pressure	14.47 *
							Habitat type	2.13 *
							Lepidoptera	4.75 *
Open-space foragers	Patch density	1.36	Patch density	1.73 *	Forest	2.39 *	Lepidoptera	15.35 *
	Human	1.24	CONTAG	1.3	Watercourse length	1.84 *	Air temperature	9.13 *
	Total Edge	1.45						
Edge foragers	Total Edge	- 0.57	Patch density	- 0.41	SHAPE_AM	1.09	Air temperature	22.46 *
	Maize fields	- 0.73	Human	- 0.37	Bocage	0.99	Diptera	4.38 *
							Coleoptera	1.69 *
							Atmospheric pressure	15.73 *
							Habitat type	4.48 *
Species richness	Rice fields	- 0.55	Bocage	0.65	Watercourse length	0.77	Air temperature	53.06 *
	SHAPE_AM	- 0.68	CONTAG	1.06	Forest	2.76	Lepidoptera	11.74 *
							Himenoptera	2.21 *
							Atmospheric pressure	16.85 *

Relation between guild activity and landscape and local variables

At the 6 km scale, the activity of the open-space foraging species tended to be positively associated with patch density. Furthermore, this relation continued at the 3 km focal scale, since a robust positive association was between the two. Also, the activity of the open-space foragers tended to be negatively related with landscape connectivity. At the smallest landscape scale (1.5 km), the activity of the open-space foraging guild was robustly and positively linked with forest cover and total watercourse length. At the local scale we found a robust, positive association between the activity of the open-space foragers and the abundance of Lepidoptera.

Concerning the activity of the edge-foragers, it tended to be higher with greater edge lengths, and lower when greater extensions of maize fields were present, at the 6 km focal scale. At the 3 km scale, we found that the activity of the edge-foraging guild tended to be negatively related to patch density. At the 1.5 km focal scale, the activity of this guild tended to be positively related with patch shape complexity, and with percentage of *Bocage* cover. At the local level, a robust positive association between the activity of the edge foragers and air temperature was found. Additionally, the activity of these species was robustly linked to the abundance of Diptera, and negatively to Coleoptera abundance and atmospheric pressure. Despite the strong associations established for the activity of edge-foragers at the local scale, the model presenting best fit only included air-temperature as an explanatory variable (Table 4.4).

Species richness

No relationships were found between species richness and landscape variables neither at the 6 and 3 km scales. At the 1.5 km scale, species richness tended to be positively associated with forest cover. However, the null model still presented the best fit (Table 4.4).

At the local scale, we found a robust relationship between species richness and air temperature. A positive tendency towards the abundance of Lepidoptera was also found, although this predictor was not included in the best model (Table 4.4).

Table 4.4 Summary of the best fitted models performed for each response variable. Focal scale, model composition, AIC and ΔAIC are given for each model. Negative associations signalled with (-) and null models represented by "Null". Explanatory variables abbreviated as: *Bocage* (Boc), forest (For), human (Hum), maize fields (Mai), rice fields (Ric), total watercourse length (Water), total edge length (Edge), patch density (PD), contagion (CONTAG), area-weighted mean patch shape index (SHAPE), habitat type (Hab), Coleoptera (Col), Diptera (Dipt), Lepidoptera (Lep), air temperature (Temp), atmospheric pressure (Apres).

Response variable	Focal scale	Model	AIC	ΔAIC
Total activity	6 km	For+Mai	477.86	0
		For+Mai+PD	477.88	0.02
	3 km	Boc+PD+Ric	445.28	0
	1.5 km	Ric+Boc	511.86	0
		Ric+Boc+Flo(-)	513.81	1.95
	Local	Temp+Dipt+Apre(-)+Hab	2207	0
		Temp	2208	1
Open-space foragers	6km	PD	150.09	0
		PD+Hum(-)	151.73	1.64
	3 km	PD+CONTAG(-)	161.6	0
	1.5 km	For+Water	161.08	0
	Local	Lep	1283	0
Edge foragers	6 km	Mai(-)+Edge	547.05	0
	3 km	PD(-)+Hum	553.19	0
		PD(-)	554.51	1.32
	1.5 km	SHAPE+Boc	508.85	0
	Local	Temp	2130	0
		Temp+Dipt+Col(-)+Apres(-)+Hab	2132	2
Species richness	6 km	Null	95.951	0
		Ric	97.416	1.465
	3 km	Null	95.951	0
		Boc(-)	96.569	0.618
		Boc(-)+CONTAG(-)	97.701	1.75
	1.5 km	Null	95.951	0
		Water	96.880	0.929
		Water+For	97.183	1.232
	Local	Temp	1040	0

4.5. DISCUSSION

Bat responses across landscape scales

Habitat heterogeneity, at least to a certain level, has been linked to higher abundance and/or diversity of several *taxa*, such as birds (MacArthur and MacArthur, 1961; Gilroy et al., 2010), small terrestrial mammals (Cramer and Willig, 2002; Dalkvist et al., 2011), and carnivores (Mestre et al., 2007; Pita et al., 2009). Bats are also no exception to this (Bernard and Fenton, 2002; Estrada and Coates-Estrada, 2002; Gorresen and Willig, 2004; Yates and Muzika, 2006; Bernard and Fenton, 2007; Ethier and Fahrig, 2011). In some situations, a matrix characterized by several interspersed patches of small size and varying land cover type seems to provide complementary resources for bats (Cramer and Willig, 2005; Ethier and Fahrig, 2011) some of them vital, such as roosting, foraging and drinking sites (Law and Dickman, 1998), within short distances.

Our results indicate that a higher number of patches per unit of area favours the activity of the species that compose the open-space foragers guild. This is supported by the robust, positive relationship, found between the activity of the open-space foragers and patch density at the 3 km focal scale, following a similar tendency at the 6 km scale. Despite not providing information on patch type, size and distribution, this landscape metric can be interpreted as a simple measure of landscape fragmentation (Dewan et al., 2012). This may reinforce the importance of the mosaic of habitats for bats if the patch types are diverse, which is likely due to the heterogeneous character of the study area.

Our findings are consistent to those of Klingbeil and Willig (2009) and Estrada-Villegas et al. (2010), who also found positive effects of fragmentation on the abundance of species adapted to forage in open areas. Habitat use is strongly dependent on species eco-morphological traits (Fenton, 1990; Schnitzler and Kalko, 2001), so bat responses to habitat fragmentation and heterogeneity are expected to vary among guilds and species. That hypothesis was supported by our results since, contrary to the open-space foragers, the activity of the edge foragers tended to be lower with higher patch densities, at least at the 3 km focal scale. Fuentes-Montemayor et al. (2013), also found a negative influence of fragmentation on edge-foraging species such as those of the genera *Pipistrellus* and *Myotis*. Additionally, Estrada-Villegas et al. (2010) found a similar influence of fragmentation on closed-habitat foragers, justified mostly by their slow and manoeuvrable flight, which makes long commuting flights energetically expensive.

Several authors have found higher levels of bat activity near linear structures and habitat edges (e.g. Verboom and Huitema, 1997; Lentini et al., 2012). Our results go in accordance with those studies. First, the activity of the edge foragers, at least at the 6 km focal scale, tended to be higher with greater edge lengths, though this was a relation not followed by open-space foraging species. Furthermore, at the 1.5 km scale, the activity of the edge-foragers tended to be higher with an increase in patch shape complexity. Greater shape complexity often implies longer boundaries between habitats (i.e. edge), reinforcing the aforesaid relationship. Contrary to our results, Fuentes-Montemayor et al. (2013) found woodland edge density to be negatively associated with the activity of *Pipistrellus* and *Myotis* species, and that the activity of these species was higher in woodland interior than in woodland edge.

Also, both total bat activity (at the 3 km and 1.5 km focal scales) and the activity of edge foraging bats (at the 1.5 km focal scale) tended to be higher when greater percentages of *Bocage* land cover were present. The greater availability of linear structures such as the typical live fences of this habitat type may provide species like *P. pipistrellus* and *P. pygmaeus* optimal foraging sites, as well as protection against predators and adverse weather conditions (Verboom and Huitema, 1997). The dense network of freshwater channels along with those hedgerows may work as a commuting route for these bats, while also providing drinking water. The positive tendencies found between the activity of edge foragers and total edge length, shape complexity and *Bocage* land cover emphasise the importance of edge habitats and linear structures for species that share the eco-morphological traits that characterize this guild – slow and energetically inexpensive flight type, average wing loading and aspect ratio, and echolocation pulses composed of both broad and narrowband components.

At the smallest landscape scale studied – 1.5 km – we found strong associations between the activity of open-space foragers and the percentage of forest cover and length of watercourses. Forest importance for European bat species is well documented, both as foraging (e.g. Vaughan et al., 1997; Russ and Montgomery, 2002; Davidson-Watts et al., 2006) and roosting (Russo et al. 2004; Dietz et al. 2009; Boughey et al. 2011) habitats, thus the importance of the amount of forest on bat activity is not surprising. Boughey et al. (2011) found that, within a small scale, roost location of *E. serotinus* (among other species) was strongly associated with the proximity of woodland patches. Species of the genus *Nyctalus* are also known to roost within woodland patches, mainly on tree holes (Dietz et al., 2009; Popa-Lisseanu et al., 2009), while *T. teniotis* often uses woodland habitats as foraging grounds (Marques et al., 2004; Rainho, 2007; Matos et al., 2011).

However, the forests of the BVL landscape are mostly *Eucalyptus* stands, which are often associated with lower animal diversity and abundance, including bats (e.g. Russo and Jones 2003; Matos 2011) and other taxa (e.g. arthropods, Zahn et al. 2009; birds, Marsden et al. 2001; Proença et al., 2010; small non-volant mammals, Carey and Johnson, 1995), and do not seem to provide suitable roosts for bats. However, these forested areas still harbour some autochthonous trees such as *Quercus* sp. that, despite having low densities, may enable the occurrence of some bat species by providing some roosts.

The strong relationship found between the activity of open-space foragers and total watercourse length reinforces the importance of riparian habitats for bats (e.g. Walsh and Harris, 1996; Grindal et al., 1999; Rainho, 2007). Freshwater courses not only provide a source of drinking water for bats, but these and the several brackish water channels present in the study area may also function as foraging grounds (Menzel et al., 2005; Rainho, 2007; Lookingbill et al., 2010) and commuting routes (Grindal et al., 1999; Fukui et al., 2006; Lloyd et al., 2006).

Bat responses at the local scale

Air temperature is one of the most limiting factors of bat activity in temperate regions, either through direct influence or subsequent food shortages during the cold winter months (Kapfer and Aron, 2007). Indeed, we found that weather conditions, particularly air temperature, strongly influence bat activity and species richness; the models presenting best fits for the activity of edge foragers and species richness only included this predictor. Within the study area, local variation in air temperature was clear, varying within the same night, between different sites, up to 6.8ºC.

We also found robust associations between prey abundance and bat activity. However, bats response to prey abundance differed between open-space and edge-space foraging bats. While the activity of open-space foragers was strongly associated with the abundance of Lepidoptera, the activity of the edge foragers was linked with the abundance of Diptera.

Open-space foragers are known to feed on Lepidoptera. *T. teniotis* seems to mainly feed on this taxa (Rydell and Arlettaz, 1994), which also constitutes a great part of the diet of *E. serotinus* (Robinson and Stebbings, 1993; Kervyn and Libois, 2008; Mikula and Cmoková, 2012). The feeding on Lepidopera by *Nyctalus* spp. has also been documented (Waters et al., 1995; Dietz et al., 2009, and references therein). This seems to justify the strong positive relationship between the activity of open-space foragers and the abundance of

Lepidoptera. On the other hand, the strong association between the activity of edge-space foragers and the abundance of Diptera may be related to the preference shown by *P. pygmaeus* and *P. pipistrellus* (the most frequently recorded species) for those prey (Swift et al., 1985; Barlow, 1997; Vaughan, 1997; Bartonicka et al., 2008).

Keystone structures and vital resources in a heterogeneous landscape

Tews et al. (2004) defined a keystone structure as "a distinct spatial structure providing resources, shelter or 'goods and services' crucial for other species". Under the light of such definition, and taking in consideration our results, we may assume that woodlands represent a keystone structure for the open-space foragers guild. Our results also suggest that *Bocage* may represent a keystone structure for the edge-foraging species.

As expected, prey abundance (for both guilds) and freshwater availability (for open-space foragers) stood out as important predictors of bat activity. Changes in food supply are considered to be one of the key factors determining spatial (Robinson and Stebbings, 1997; Kusch and Idelberger, 2005) and seasonal (Bartonicka and Zukal, 2003; Meyer et al., 2004; Ramos Pereira et al., 2010) variation in bat activity. Our results suggest that, within the heterogeneous landscape of BVL, bat activity is not mainly limited by land cover type, but rather by prey abundance and weather conditions. Therefore, we may assume that the habitat types that shape the BVL matrix provide a high complementation of resources, though woodlands and *Bocage* probably act as keystone structures.

Conclusions

Bat activity and distribution within the heterogeneous landscape of the BVL seems to be under the influence of several environmental factors, acting at different levels and scales. Overall, bats seem to respond to different factors, from wider scales where landscape physiognomy variables (i.e. fragmentation and edge length) are the most influencing ones, to a finer one where keystone habitats and vital resources (e.g. roosting sites and freshwater availability) are the limiting factors. At a local scale, prey availability and weather conditions (mainly air temperature) are the main factors dictating site selection. Our results support the findings of several studies that described scale-dependent effects of environmental variables on various aspects of the ecology of bats (e.g. Gorresen et al., 2005; Perry et al., 2008; Pinto and Keitt, 2008; Klingbeil and Willig, 2009; Ethier and Fahrig, 2011) and other taxa (e.g. plants, Graham and Knight, 2004; Okland et al., 2006;

fish, Yeager et al., 2011; small non-volant mammals, Morris, 1992; and marsupials, Lyons and Willig, 2002).

Bats seem to be sensitive to local resource availability and distribution, while simultaneously reacting to broader landscape features. However, the smallest and wider scales to which an organism responds depends on the animals' eco-morphology (i.e. size, mobility, life-history traits) since a given mosaic can be interpreted in a "fine-grained" way by a certain species, and in a "coarse-grained" fashion by others (Kotliar and Wiens, 1990), sometimes even in the same family or order. Furthermore, different species may respond to distinct landscape features, depending on those eco-morphological traits. Our results revealed different influencing variables on the activity of the open-space and edge-space foraging guilds. Similar results were obtained by Klingbeil and Willig (2009), who found guild-specific responses to forest fragmentation. Gorresen et al. (2005), Perry et al. (2008), Pinto and Keitt (2008) and Ethier and Fahrig (2011) also found species-specific responses to distinct landscape features, such as patch size, shape and proximity, forest cover, and woodland characteristics. Some of these species-specific responses may be masked by our analysis at the guild level, since it mostly reflects the responses of the dominant *taxa*. Further work, and more robust data is necessary to assess those species-specific responses in the BVL landscape, particularly to closed-habitat foragers, since we were not able to investigate their interaction with the heterogeneous landscape of BVL. Most likely, landscape fragmentation and heterogeneity will be found to negatively affect these species, since they are strictly associated with forested habitats, and due to their eco-morphological traits (e.g. slow and energetically expensive flight) they have low mobility, thus making commuting between distant patches too costly. Still, our approach is certainly more detailed than one performed, for instance, at the assemblage level, because it provides some insight on the differences between functional groups (Klingbeil and Willig, 2009).

Our study underlines the importance of multi-scale approaches to effectively assess the influence of landscape composition and physiognomy on bat activity. Furthermore, a deeper look into species-specific and/or guild responses is essential. In fact, such analyses may enable the identification of the most important landscape characteristics for the studied *taxa*, as well as of keystone structures and vital resources, facilitating the recognition of important conservation areas, and the design of effective conservation plans as an important support for land management.

Chapter 5

General Discussion

5. GENERAL DISCUSSION

5.1 STUDY DESIGN AND MAIN FINDINGS

BVL is a coastal wetland. Here the landscape is composed by a matrix of natural, semi-natural and human-altered habitats. Despite being known as a rich area in terms of biodiversity (Brito et al., 2010), little is known about the spatial and seasonal patterns of vertebrate distribution, and about the factors that underline those patterns. In this study, we assessed several aspects of the ecology of bats, so that the interaction between this group of animals and the heterogeneous landscape of BVL could be better understood.

Firstly, we investigated the composition and structuring patterns of bat assemblages, and compared those patterns among seasons and among the main habitats that shape the landscape. Secondly, we assessed the spatial dynamics of bat activity, so that the habitat preferences of bats could be unveiled, taking into consideration their differences in foraging strategy and morphology. Furthermore, we also studied differences in bat activity across seasons. Subsequently, it was important to focus on the processes that underline those patterns. Thus, we assessed the influence of several features acting at local and landscape on the patterns of bat richness and activity. Moreover, we investigated the scale-dependency of the response given by bat activity and richness, by analysing the effects of the features across a gradient of focal scales. Finally, we analysed the different responses given by different bat guilds, composed by species with distinct eco-morphological traits, to landscape and local features.

The main findings/conclusions obtained through each of the abovementioned steps are:

Bat assembly structuring across habitats and seasons

i) Bat assemblage structure and composition was found to be similar among the eight habitat types studied;

ii) A significant variation in bat diversity, richness and evenness was found throughout the study period.

Spatial and seasonal patterns of activity

i) Overall, few differences in the activity patterns of the different bat species across habitats were found;

ii) Higher activity levels were detected in urban sites (*P. pygmaeus*), Bocage (*P. pygmaeus* and *P. pipistrellus*) and forests (*N. leisleri*);

iii) Bat activity in the different habitat types varied throughout the study period, probably due to shifts in prey availability.

Conclusions

i) Bats seem to interpret the BVL landscape matrix as a whole, rather than selecting or exploiting the different habitat types individually;

ii) The heterogeneous landscape that characterizes the BVL region seems to provide a mosaic of opportunities for bats, which freely exploit the resources across different land cover settings and according to their temporal variation.

Bat responses across landscape scales

i) Bat activity responses to landscape features are both scale- and guild-dependent;

ii) At broader scales, bats seem to respond to mainly to landscape physiognomy features, such as fragmentation, patch shape complexity and edge length, while at finer scales, landscape composition features such as land cover proportions and water availability, seem to be the most influencing ones;

Bat responses at the local scale

i) Locally, bat activity is driven mainly by weather conditions (particularly air temperature) and by prey abundance.

Conclusions

i) Bats seem to respond to different factors, from wider scales where landscape physiognomy variables (i.e. fragmentation and edge length) are the most influencing ones, to a finer one where keystone habitats and vital resources (e.g. roosting sites and freshwater availability) are the limiting factors;

ii) Site selection is not mainly limited by land cover type, but rather by prey abundance and weather conditions;

iii) Woodlands and Bocage may be regarded as “keystone structures” for bats within the BVL landscape.

5.2 BATS AND THE HETEROGENEOUS LANDSCAPE OF BAIXO VOUGA LAGUNAR

Since bat assemblages of the sampled habitat types were similar, and almost no species-habitat associations were established, bats seem to exploit all habitat types present in the BVL landscape. This may be partly explained by the generalist character of some of the recorded species (e.g. *E. serotinus*, Rainho, 2007; *N. leisleri*, Lundy and Montgomery, 2010; *P. pipistrellus*, Russo and Jones, 2003). Furthermore, many species may depend on multiple habitats to fulfil their daily and seasonal needs, especially to deal with different requirements along the various stages of their life-cycle stages (Law and Dickman, 1998; Lookingbill et al., 2010). An increase in the structural complexity of a habitat mosaic leads to the availability of more ecological niches, and promotes several distinct opportunities for resource exploitation (habitat heterogeneity hypothesis, Bazzaz, 1975; Tews et al., 2004). Since bats are highly vagile, able to readily move between adjacent patches within the BVL heterogeneous landscape, they are probably able to exploit the different resources provided by different patches, and according to their temporal fluctuations. The BVL landscape contains different patch types, potentially providing adequate foraging and roosting habitats, as well as vital resources such as freshwater and prey, all located within short distances (landscape complementation, Dunning et al., 1992); this is probably the reason why land cover influence was shown to be relatively reduced.

5.3 'KEYSTONE STRUCTURES' AND VITAL RESOURCES

From the analysis performed, three habitat types stand out from the remaining, concerning the levels of bat activity. Firstly, urban sites revealed higher levels of activity of *P. pygmaeus*, and a positive tendency to higher levels of total bat activity and of edge foraging species. Foraging in urban environments is not an unusual behaviour for several species of bats, since high densities of prey may occur, particularly around streetlights (Gaisler et al., 1998; Rydell, 1992; Avila-Flores and Fenton, 2005). The proximity of human settlements to woodlands and riparian habitats in the BVL landscape, may also provide these species with additional suitable foraging habitats.

The activity of *N. leisleri* was positively related to forest sites, and a strong positive relation was found between the activity of the open-space foraging guild and forest cover, at the finest landscape scale approached. The importance of woodlands for European bat species is well documented, both as foraging (e.g. Vaughan et al., 1997; Russ and Montgomery, 2002; Davidson-Watts et al., 2006) and roosting (Russo et al., 2004; Dietz et

al., 2009; Boughey et al., 2011) habitats. Of the open-space foraging species, *E. serotinus* was found to select roosts closely located to woodland patches (Boughey et al., 2011), while species of the genus *Nyctalus* usually roost within them, mainly on tree holes (Dietz et al., 2009; Popa-Lisseanu et al., 2009). *T. teniotis*, on the other hand, its known to use these habitats as foraging grounds, where it usually feeds above the canopy (Marques et al., 2004; Rainho, 2007; Matos et al., 2011).

Laslty, higher levels of activity of both *P. pygmaeus* and *P. pipistrellus* were found in *Bocage*, and linked to higher activity levels of the edge foraging guild at two focal scales. The greater availability of linear structures such as the typical live fences of this habitat type may provide these species optimal foraging sites, as well as protection against predators and adverse weather conditions (Verboom and Huitema, 1997). The dense network of freshwater channels along with those hedgerows may work as a commuting route for these bats, while also providing drinking water.

Following the definition of "keystone structure" provided by Tews et al. (2004), the classification of these habitats as keystone structures for bats within the heterogeneous landscape of BVL seems reasonable.

As expected, vital resources stood out as important predictors of bat activity. The activity of both guilds was influenced by prey abundance (Diptera for the edge-foraging species, and Lepidoptera for the open-space foragers), and the activity of the open-space foragers was also positively related to freshwater availability. Changes in food supply are considered to be one of the key factors determining spatial (Robinson and Stebbings, 1997; Kusch and Idelberger, 2005) and seasonal (Bartonicka and Zukal, 2003; Meyer et al., 2004; Ramos Pereira et al., 2010) variation in bat activity. Our results revealed that prey abundance and weather conditions, particularly air temperature, despite related, were the variables that better explained the seasonal changes in bat activity in the BVL. Furthermore, prey abundance seemed to influence more the process of site selection than land cover type, emphasising the opportunistic character of several species.

5.4 SCALE- AND GUILD-DEPENDENCY OF THE RESPONSES GIVEN BY BATS

We found that bat activity and richness, within the heterogeneous landscape of BVL, seem to be influenced by landscape physiognomy and composition, and regulated by weather conditions and prey abundance. Furthermore, we found that the responses given by bats to these features changed across a scale gradient. The results obtained in this study support the findings of several works that described scale-dependent effects of environmental variables on various aspects of the ecology of bats (e.g. Gorresen et al., 2005; Perry et al., 2008; Pinto and Keitt, 2008; Klingbeil and Willig, 2009; Ethier and Fahrig, 2011) and other taxa (e.g. plants, Graham and Knight, 2004; Okland et al., 2006; fish, Yeager et al., 2011; small non-volant mammals, Morris, 1992; and marsupials, Lyons and Willig, 2002). However, the eco-morphological traits of an organism, such as size, mobility and life-history traits, limit the scale to which it responds to environmental features. In fact, a given mosaic can be interpreted in a “fine-grained” way by a certain species, and in a “coarse-grained” fashion by others (Kotliar and Wiens, 1990), therefore species with different eco-morphological traits are expected to respond differently. Accordingly, species differing in morphology and hunting strategies were found to respond to different landscape features within the BVL. Similar results were obtained by Klingbeil and Willig (2009), who found guild-specific responses to forest fragmentation. Gorresen et al. (2005), Perry et al. (2008), Pinto and Keitt (2008) and Ethier and Fahrig (2011) also found species-specific responses to distinct landscape features, such as patch size, shape and proximity, forest cover, and woodland characteristics.

5.5 CONSERVATION IMPLICATIONS

Future strategies designed towards the conservation of bats within the BVL landscape, or on heterogeneous landscapes elsewhere, should include a multi-scale approach, so that it can effectively manage both landscape composition and physiognomy features that promote the activity and richness of bat species. Furthermore, since species respond differently to landscape features, species-specific analysis should be performed. Such analyses may enable the identification of the most important landscape characteristics for the studied *taxa*, as well as of keystone structures and vital resources, facilitating the recognition of important conservation areas, and the design of effective conservation plans as an important support for land management. However, species-specific approaches often involve greater costs and human resources, and are frequently time-

consuming. Thus, alternatively, a guild-specific approach may be applied, since it provides information for a group of species sharing eco-morphological traits. Nonetheless, guild-level approaches may mask the rarest species responses, as it reflects mainly the responses of the dominant *taxa*. Therefore, the identification of umbrella species is critical for prioritizing conservation areas (Rainho and Palmeirim, 2013).

Woodlands (forest patches and *Bocage*) were found to be the most important habitats for bats within the BVL landscape, probably acting as keystone structures for these animals. These habitats may provide adequate roosting and foraging habitats, while additionally offering commuting routes and freshwater, through the linear structures and water courses found on *Bocage*. However, the absence of broadleaved woodlands may negatively affect the strict forest-dwelling species such as *B. barbastellus* and *Plecotus* spp., which were rarely recorded during this study. Although the detectability of bats sampled is lower within forest patches (Walsh et al., 2004) where these species forage and roost, the few recordings we got may also suggest they are rare within the BVL landscape. Therefore, the creation/restoration of broadleaved woodlands may be adequate to provide additional roosting and foraging habitats for these species, while also favouring other bats that usually roost in such habitats, such as those of the genus *Nyctalus* (Dietz et al., 2009; Popa-Lisseanu et al., 2009).

Lastly, the results obtained in this study revealed that higher levels of the activity of some species were related to edge length and to *Bocage* cover, which is composed by a dense network of linear structures. Since a great proportion of the BVL landscape is composed by maize fields, characterized by great areas of crop fields, managed in a somehow intensive fashion, the promotion of hedgerows and tree lines around them may also favour bat activity and occurrence. Linear elements such as those, have also been found to positively influence bat activity in agricultural areas in other studies (Verboom and Huitema, 1997; Russ and Montgomery, 2002; Fuentes-Montemayor et al., 2011; Lentini et al., 2012). The creation of these structures around the larger crop fields may provide foraging and roosting habitats for bats, as well as protective commuting routes in these open areas. Furthermore, promoting the activity of insectivorous bats near crop fields may result in a better control of insect pests species, thus resulting in a direct service to human populations.

5.6 FUTURE WORKS

Future research on bat ecology in the BVL should focus on species-specific responses to landscape composition and physiognomy. Such approaches may elucidate the differences among species, and enable the assessment of the responses given by rare species. Furthermore, these analyses may allow the identification of umbrella species, and therefore provide essential information for future conservation plans.

Since roost availability is one of the most limiting factors for bat distribution within a region, further studies should be made about roost availability within the BVL landscape, particularly for species that depend on woodlands for roosting, namely species from the genera *Nyctalus* and *Plecotus*, and for *B. barbastellus*.

Radio-tracking studies should also be developed, so that more information could be gathered on species movements within this heterogeneous landscape, giving insight about species home-ranges and core areas, as well as about potential seasonal migrations of different species of bats.

Lastly, studies about the ecosystem services provided by bats in this agricultural landscape should be performed, focusing on the effect insectivorous bats have in pest control, and on the consequent benefits obtained by land owners. Bat-boxes could be setup on some of the fields, thus promoting bat roosting and foraging activity in the surrounding areas, and total production compared to control crops. Additionally, production values should also be compared between crops under the influence of pesticides and control ones. By comparing total productions (or the losses due to insect herbivory), and the costs of bat-boxes versus pesticide use, both pest control service importance and its economic advantages could be assessed. However, monitoring the more specialized species would be essential, since bat boxes usually favour the most species that are known generalists.

Chapter 6

REFERENCES

6. REFERENCES

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